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Estimation of cod (*Gadus morhua*) growth in NAFO Subdiv. 3Ps and Divs. 3KL in 1997-1999 from tagging experiments.

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Abstract

We develop a model for estimating growth of Atlantic cod in NAFO Subdivision 3Ps and Divisions 3KL during 1997-1999. We use tag-returns from the commercial, sentinel, and food fisheries in these regions during 1997-1999. The returns are from numerous tagging experiments conducted in 3Ps and 3KL during 1997-1999. Many of the tags that are returned supply the length of the fish at capture, and we use this information to estimate growth based on known lengths-at-release and times-at-liberty. We use the Von Bertalanffy growth model, modified to accommodate seasonal variations in growth. We also incorporate a measurement bias component in our estimation because the tag-return data suggest that there is some bias in the lengths-at-capture reported by fishermen. The basic approach we use has been studied fairly extensively in the fisheries literature, and we present a review of this literature. Important biases in estimating growth from tagging data have been identified in the literature, and we assess the magnitude of the bias in our analysis using a simple simulation. The conclusion from our simulation is that the bias may not be substantial for our population. We use the estimated model to predict cod growth for times-at-liberty ranging from 0-3 years, and for fish lengths ranging between 40 and 90 cm. For example, we estimate that a 40 cm fish will grow 22 cm during 1997-1999, but in the same period a 90 cm fish will grow only 10 cm.

Résumé

Nous avons élaboré un modèle pour l'estimation de la croissance de la morue de l'Atlantique de la sous-division 3Ps et des divisions 3KL de l'OPANO de 1997 à 1999. L'information des retours d'étiquettes de marquage obtenue des pêches commerciale, sentinelle et alimentaire a été utilisée dans cette région pour la même période. Les étiquettes provenaient de diverses expériences de marquage faites dans la même zone et au même moment. Bon nombre des étiquettes obtenues étaient accompagnées de la longueur du poisson à la capture et nous avons utilisé cette donnée pour estimer la croissance à partir de la longueur connue au moment de la remise à l'eau et de la période s'étant écoulée avant la recapture. Nous nous sommes servis du modèle de croissance de Von Bertalanffy, modifié pour tenir compte des variations de croissance saisonnières. Nous avons aussi ajouté à nos estimations une composante pour le biais des mesures car les données des retours d'étiquettes portent à croire à un certain biais du niveau des longueurs à la capture signalées par les pêcheurs. La démarche que nous avons utilisée a fait l'objet d'études assez exhaustives mentionnées dans la littérature et nous en présentons un examen. Des biais importants affectant l'estimation de la croissance à partir des recaptures de poissons marqués sont mentionnés dans les publications et nous en avons évalué l'importance pour notre analyse à l'aide d'une simulation simple. Selon cette dernière, le biais ne serait pas important pour la population étudiée. Nous avons appliqué le modèle à la prévision de la croissance des morues pour des périodes de liberté allant de 0 à 3 ans et pour des longueurs de 40 à 90 cm. Ainsi, pour la période de 1997 à 1999, nous avons estimé à 22 cm la croissance d'un poisson de 40 cm, mais à seulement 10 cm celle d'un poisson de 90 cm.

1 Introduction

It is possible to estimate the exploitation rate by a commercial fishery using data from fish tagging experiments. Essentially, the fraction of tags caught in the commercial fishery and returned by fishermen provides an estimate of the fishery exploitation rate, assuming that the fishery equally exploits tagged and un-tagged fish, and that the tag reporting rate is known. The exploitation rate can then be used, in conjunction with estimates of the total landings by the fishery, to estimate stock size (see Cadigan and Brattey, 2000).

The cod fisheries in NAFO Subdivision 3Ps and Divisions 3KL are size-selective; that is, not all sizes of cod are exploited equally. The differences in exploitation are usually expressed as a function of fish length, so that the exploitation rate depends on the length of fish when captured. Selectivity has been considered by Hoenig and Myers (1997), although they only examined tag-returns within a short time following release, in which case growth is not important. We use all of the tags returned from 3Ps and 3KL during 1997-1999 to maximize precision; however, growth is important when fish are caught after a relatively long time-at-liberty. For the tagging experiments we consider length is accurately measured by trained technicians when fish are tagged; however, length measurements are not available for many of the tagged fish recaptured by fishermen. In addition, the methods used by fishermen and other individuals to measure length have considerable measurement error. This is evidenced by numerous negative estimated growth increments between the time-of-release and the time-of-capture. We need better estimates of fish length at the time-of-capture to get more reliable estimates of the length component (i.e. selectivity) of exploitation.

In this paper we develop a model for estimating growth of Atlantic cod in 3Ps and 3KL during 1997-1999. We use tag-returns from the commercial, sentinel, and food fisheries in these regions during 1997-1999. The returns are from numerous tagging experiments conducted in 3Ps and 3KL during 1997-1999. These experiments are described elsewhere (Brattey 1999; Brattey et al. 1999; Brattey 2000). The purpose of this paper is to specify a model that we can use to estimate the length of a fish at a known time-of-capture. This information will be used in Cadigan and Brattey (2000) to estimate the length-selectivity of recent commercial cod fisheries in 3Ps and 3KL.

2 The data

We analyze the tag-returns from 55 tagging experiments conducted in 3Ps and 3KL during 1997-1999. Most cod for tagging were captured with hand-lines, but some trap-caught and otter-trawled cod were also tagged. The length of each cod (nearest cm) was recorded. Only cod with a fork length exceeding 45 cm and in excellent condition were tagged and released. For analysis, groups of cod tagged in the same general area over a time frame of a few days to weeks were classified as a single experiment which was assigned a four digit sequential identifier; the first two digits representing the year of capture and the second two digits incrementing annually from 01 onwards (i.e. 9701, 9702...). The locations of experiments are shown in Figure 1.

For our growth analysis we used only those tags that were returned with an estimated length and a capture date. We grouped capture times into weeks, to be consistent with other analyses of this data. We grouped tag-returns into three broad geographical areas, similar to those in Cadigan and Brattey (1999). We use these regions to investigate whether growth rates vary geographically. The regions (see Figure 1) are denoted as

Region 1: 3Ps
Region 2: Southern 3L
Region 3: Northern 3L and 3K

Southern 3L consists of units 3Lf, 3Lj, and 3Lq, which is the inshore area covering St. Mary's Bay up to and including Conception Bay. Northern 3L and 3K includes Trinity Bay (3Lb), Bonavista Bay (3La) and areas northwards (3K).

Some fish in 3Ps and 3KL migrate between regions. For our growth analyses we only use tag information from fish that were captured in the same region they were released in. We assume that if a fish is tagged and released in a region, and also caught there, then that fish has spent most of its life in that region. If there is inter-regional variation in growth rates that is determined only by factors existing in the region (so that a fish that migrates into a region assumes the growth rate for that region) then the subsetting procedure we use should tend to isolate fish that have experienced only one regional growth rate. A total of 1798 tags were available from fish tagged and released in 3Ps and 3KL in 1997-1999. Of these, 1578 were returned from the same region of release. We estimate growth from the information fishermen supplied with these 1578 tags.

There are a some known problems with these data that we wish to highlight. On several occasions tags have been received with information that we known is not correct. We speculate that sometimes fishermen do not immediately record all the information (length, date, place of capture) about the tagged fish that they caught, and they guess about some of the required information when they send tags in later. Such guesses can be highly inaccurate. Another problem is that for some of the tag-returns, length-at-capture was entered into the tagging database as missing if it was less than the length-at-release. This will result in biased measurements of fish growth, which we must also accommodate in our model. In future we will remove this bias component by going back over the recapture lengths and entering all of them into our database, irrespective of whether they are smaller than the length-at-release.

3 Exploratory and nonparametric analyses

The data set we use for estimating fish growth has not been examined previously, so initially we conducted some exploratory analyses to determine the potential growth signal in these data, and to elucidate potential problems in using these data to estimate growth.

Growth is primarily a function of time-at-liberty and fish length. Naturally, we expect a fish to grow less in a short period of time than in a longer period of time. Also, we expect the growth rate to decrease as growth increases; that is, for a fixed period of time we expect

a small fish to grow more than a large fish. Our first analysis is to examine the estimated growth increments over time, for ten length-at-release intervals. These intervals were chosen so that there is a reasonable amount of data to explore the relationship between growth, length, and time-at-liberty. The estimated growth increment (G) is defined as

$G \equiv$ the reported length at the time-of-capture minus the known length-at-release

Note that G is the response variable we consider. The observed G's are shown in Figs. 2-4. Growth may also vary geographically which is why we stratified these plots by region. The plots indicate that most (70.3%) of our data is for region 1 (see Fig. 2). Only 2.2% of the tags were returned from region 2 (see Fig. 3), and 27.5% were returned from region 3 (see Fig. 3). These figures also show a large number of negative G's. For all three regions 32% of the tagged fish caught were reported to have decreased in length, which is not possible.

We assume that growth (in length) is a non-decreasing function of time-at-liberty (t), so negative growth can result only from errors in the recapture length measurements obtained from fishermen. In Figs. 2-4 the solid lines mark estimates from local linear regression smoothers (see Cleveland and Devlin, 1988). We used the S-plus loess function for smoothing. The numbers at the top of the plots are the smoother predicted growth increments at $t = 2, 20, 60$ and 120 weeks. These values of t were arbitrarily chosen to demonstrate the relationship between average reported growth and t. Broadly speaking these data do suggest some of the growth features we expect; that is, growth increases with t, and also with length-at-release (l_r). Figs. 2-4 do not suggest vastly different growth rates between regions. Figs. 2 and 4 suggest that there is possible bias in the growth measurements because the smoother predicted growth at $t = 2$ is usually negative, and this trend increases with length. We expect that little or no growth occurs within the first two weeks following release, so Figs. 2 and 4 suggest that fishermen tend to under-report fish lengths, and the amount of under-reporting may depend on the size of the fish.

To further investigate this bias we examine growth within 5 weeks following release (i.e. $t \leq 5$), which we denote as G^*. We choose this time scale so that our analyses are based on reasonable sample sizes. Note that some growth may occur within 5 weeks, and otherwise we expect G^* to be more positive than negative because of the data recording problem mentioned in **Section 2.1** (i.e. some negative G's were not entered into the database). We first examine the regional relationship between G^* and l_r. These data are plotted in Fig. 5 for regions 1-3 in the upper three panels, and for all regions in the bottom panel. There is a consistent trend in G^* versus l_r in regions 1 and 3; that is, G^* is approximately zero for $l_r < 60$ cm, and decreases to about -5 cm for $l_r > 70$ cm. This suggests little or no bias in G for $l_r < 60$ but a bias of -5 cm for $l_r > 70$. The data for region 2 are probably too sparse to detect this trend.

Overall the regional nonparametric regressions are not significantly different. Some statistics from the regressions are presented in Table 1. The statistic proposed by Cleveland and Devlin (1988) that we use to test whether there are significant regional differences

Table 1. Statistics from the regional nonparametric regression analyses of cod growth increments within 5 weeks after release, and length-at-release. The sample size is n. SSE is the regression error sum of squares, H denotes the hat matrix, $\delta_1 = tr\{(I-H)(I-H)'\}$, and $\delta_2 = tr\{(I-H)(I-H)'\}^2$

Region	n	SSE	$tr(H)$	δ_1	δ_2
1	81	3339.79	5.46	75.06	74.73
2	13	13.80	6.14	6.27	5.98
3	128	3330.59	5.84	121.64	121.29
sum	222	6684.18	17.44	202.97	202.00
all regions	222	6932.97	5.74	215.76	215.42

in the relationship between G^* and l_r is

$$F_{obs} = \frac{(SSE_{all} - SSE_{sum})/(\delta_{1,all} - \delta_{1,sum})}{SSE_{sum}/\delta_{1,sum}}, \qquad (1)$$
$$= \frac{248.79/12.97}{6684.18/202.97} = 0.583.$$

If $G^* = f(l_r)+\varepsilon$, where $f(l_r)$ is a smooth function in l_r and $Var(\varepsilon)$ is constant, then F has an approximate F-distribution. The loess function does not output all of the information required to compute the numerator degrees of freedom suggested by Cleveland and Devlin (1988) for this F statistic; however, a good approximation is $df_{num} = \delta_{1,all} = 12.97$. The loess function does produce the denominator degrees of freedom, which is $df_{den} = \delta^2_{1,sum}/\delta_{2,sum} = 203.94$. Using these values we compute $\Pr(F > F_{obs}) = 0.866$, and this p-value suggests that there is little evidence in our data that the bias in G^* as a function of l_r varies between the three regions.

The bias in our measurements of G may also change annually. One such cause could be an annual change in the number of negative growth increments entered as missing in our database. To investigate for this we examine the relationship between G^* and l_r for each year. Scatter plots of these data are presented in Fig. 6. The smoothers suggest substantial annual variation in the bias as a function of l_r. We assess the statistical significance of the annual variation using (1). The regression statistics are presented in Table 2, and $F_{obs} = 2.2$. The $\Pr(F > F_{obs}) = 0.013$, and this suggests that the annual differences in the relationship between bias and l_r are statistically significant.

A related problem is whether the bias changes within a year. We propose a seasonal model for fish growth later, and we wish to be sure that the seasonal effects we demonstrate are related to growth and not bias. Scatter plots of bias versus tag-return week are presented in Fig. 7. There is little evidence of a seasonal trend in bias, especially in 1999 which is the year in which most of our data comes from.

Another potential source of variation in bias are fishing gear effects. Fishermen may know more precisely the length of fish that a particular type of gear (e.g. gillnets) has

Table 2. Statistics from the annual nonparametric regression analyses of cod growth increments within 5 weeks after release, and length at release. The sample size is n. SSE is the regression error sum of squares, H denotes the hat matrix, $\delta_1 = tr\{(I-H)(I-H)'\}$, and $\delta_2 = tr\{(I-H)(I-H)'\}^2$

Year	n	SSE	$tr(H)$	δ_1	δ_2
1997	43	1359.72	5.55	36.96	36.64
1998	26	558.42	5.26	20.26	19.96
1999	153	4231.22	5.78	146.71	146.36
sum	222	6149.36	16.59	203.93	202.96
all years	222	6932.97	5.74	215.76	215.42

caught, compared to other types of gear (e.g. traps). In this case if a fishermen makes a guess about the length of a fish then the guess would tend to be more accurate if the fish was caught in a gillnet compared to a trap. In Fig. 8 we present boxplots of G^* for each type of gear used in 3Ps and 3KL. If gear type is not reported then it is coded as unknown, while the "other" category represents a wide variety of gears that are occasionally used. Only 2% of the data were from "other" gears. The majority of the tags were from fish caught by gillnets (73%). We tested whether the bias (e.g. $E(G^*)$) depended on gear type using a standard ANOVA procedure, and the p-value is 0.45. This indicates no significant difference in bias among gear types.

4 Growth model

In the previous section we have demonstrated that the growth increment data from tag-returns have the characteristics we expect, but also that there will be some additional challenges in modelling this data because of bias. In this section we present a review of the literature relevant to our problem, and then propose a parametric growth model suitable for our data.

Our notation is somewhat nonstandard compared to that used in the fisheries literature. We conform to the standard practise of using Greek symbols for parameters that are to be estimated. We use upper case for random variables, and lower case for scalar fixed quantities, like observations. If a letter or symbol is followed by a $(\cdot)$ then that indicates it is a function of $(\cdot)$, and one has to look to the right to determine what is random or not.

4.1 Review

There is an extensive amount of literature related to estimating growth. We focus on the literature dealing with growth analyses based on individual fish growth increment data.

The other important approach to estimating fish growth is based on comparing time-series of estimates of mean length-at-age from sampling programs. The time-series are usually, but not always, annual. We do not attempt a comprehensive literature review here, but present information to convey the common issues that other researchers have dealt with, as well as assess the relevance of these issues to our method of estimating growth.

A review of several growth models useful for fish populations is presented in both Seber and Wild (1989) and Gamito (1998). The Von Bertalanffy equation (VONB)

$$L(a) = \lambda_\infty(1 - e^{-\kappa a}) \tag{2}$$

is commonly used in fisheries. In this model $L(a)$ denotes the length at age a, and λ_∞ denotes the length that is approached as $a \to \infty$. A fairly detailed mathematical description of the derivation of a generalized version of (2) is given by Bhattacharya (1966). Chen et al. (1992) concluded that the VONB model proved to be the best growth model among a variety of polynomial alternatives in a study 16 fish populations; however, the VONB model is not without opponents (see Roff, 1980).

For growth increment data the common form of the VONB equation used (see Fabens, 1965) is

$$G(t) = (\lambda_\infty - l_r)(1 - e^{-\kappa t}), \tag{3}$$

where $G(t)$ is the growth that has occurred over a time interval t. Recall that l_r was defined as the length-at-release (i.e. at $t = 0$). It is easy to see from (3) that $G(0) = 0$, and as $t \to \infty$ $G(t) \to \lambda_\infty - l_r$; that is, length $= G(t) + l_r \to \lambda_\infty$ as $t \to \infty$. This is exactly what (2) says. Note that $\partial G(t)/\partial t = G'(t) \propto G(\infty) - G(t)$ which suggests that smaller fish should grow faster than larger fish. Hence, the VONB equation has the basic feature we require for a growth model. Estimation of (3) using nonlinear least squares is commonly referred to as Fabens' method.

Much of the literature we found concerning estimation using (3) with tagging data concerned the effect of individual variability in the VONB parameters. Individual variability is modelled by assuming that each fish has its own VONB growth curve with parameters $L_{i\infty}$ and K_i. Population variability in $L_{i\infty}$ and K_i is usually modelled by assuming that these parameters are random; that is, $L_{i\infty}$ is random with mean μ_∞ and variance σ^2_∞, and K_i is random with mean κ and variance σ^2_κ. It is sometimes also assumed that $L_{i\infty}$ and K_i are correlated. We first deal with the case when the growth rate before tagging is unrelated to the growth rate following tagging, then we consider the case when growth rates before and after tagging are related.

Remark 1 *We use the i subscript to emphasize that the parameters are different for each individual; however, these random parameters are independent and identically distributed (iid) so we drop the i subscript when referring to expectations that are the same for all the $L_{i\infty}$'s and K_i's.*

Researchers have realized that if the growth parameters are random in (3) then the growth function $G^*(t) = (\mu_\infty - l_r)(1 - e^{-\kappa t})$ differs from $E\left[(L_\infty - l_r)(1 - e^{-Kt})\right]$, and

that estimators of μ_∞ and κ obtained using nonlinear least squares based on $G^*(t)$ have asymptotically non-negligible biases. Sainsbury (1980) has shown that the bias is positive for μ_∞ and negative for κ (see also Maller and deBoer, 1988). The biases can be considerable when using the growth increment model (3) rather than (2). The magnitude of the bias depends on the values of μ_∞, κ, σ^2_∞ and σ^2_κ. Sainsbury (1980) presented one example where the bias in predicting mean length was 13% when an age-length relationship was constructed from the analysis of growth increment data. Unbiased estimation is possible using $G^*(t)$ when growth before tagging is unrelated to growth following tagging only if $\sigma^2_\kappa = 0$. For this situation Kirkwood and Somers (1984) proposed a weighted least-squares approach, and Somers and Kirkwood (1991) extended this approach to include random error in length measurements. Xiao (1994) considered the case when L_∞ and K have a bivariate normal distribution, and concluded that correlation between L_∞ and K may not be that important. For estimation Xiao (1994) used (3) with measurement error in the growth increment.

Other authors have pointed out that in the stochastic setting when growth is the same before and after tagging then serious biases may result even if K is not random. Let L_r be a fishes length at age a when released, and L_c be a fishes length at age $a+t$ when captured. If these lengths are given by the VONB stochastic growth model:

$$\begin{aligned} L_r &= L(a) + \varepsilon_1 \\ &= L_\infty(1 - e^{-Ka}) + \varepsilon_1, \\ L_c &= L_\infty\left\{1 - e^{-K(a+t)}\right\} + \varepsilon_2, \\ &= \{L_\infty - L(a)\}\,(1 - e^{-Kt}) + \varepsilon_2, \end{aligned} \tag{4}$$

where the ε's are iid measurement errors, then $E(L_c - L_r)$ does not equal $G^*(t)$ when $Var(\varepsilon) > 0$, even if $\sigma^2_\kappa = \sigma^2_\infty = 0$. The expected difference is importantly different in that it involves the age-at-release, which is usually unknown.

Francis (1988) considered (2) and (3) to be different models, although most of his interpretations of the differences were based on the fact that (2) and (3) are usually used with different types of data; that is, (2) is used with time-series of mean lengths-at-age, and (3) is used with samples of measurements of growth increments over time. Interestingly, Sainsbury (1980) also contained a discussion of the effects of an animals age on a growth increment analysis. He predicted that, when more than one cohort is present in the population, the effect is to introduce a nonlinearity in the relationship between growth increment and initial length. He also felt that without age-composition information there is little that can be done, except to recognize that sources of variation are present in the data that cannot be controlled for.

James (1991) argued that there can only be one growth model given by (2), and that (3) is "merely a construct to be used for estimating parameters in that model". James (1991) showed that when there is measurement error in both L_r and L_c, or when $\sigma^2_\infty > 0$ or $\sigma^2_\kappa > 0$, then the estimating equations derived from least squares minimization of $g = l_c - l_r$ and (3) are not unbiased. Unbiased estimating equations are usually required for estimators to be consistent. James (1991) proposed unbiased estimating equations

that were found to perform well in simulations (see also Kimura et al, 1993) when the time-at-liberty varied over a wide range. These new equations are not unbiased when $\sigma_\kappa^2 > 0$; however, James (1991) also presented some limited simulations that suggested the bias in the estimators may be low even if σ_κ^2 is large. The new point from James (1991) is that measurement error in lengths, in addition to intrapopulation variability in K, can lead to asymptotically biased estimators. Also, James (1991) suggested that variability in K may not be as important as measurement error and variability in L_∞, at least not for the estimators he proposed.

Palmer et al. (1991) considered both errors in length measurements and intrapopulation variability in the VONB equation, including correlation between L_∞ and K. They postulated a stochastic growth model with individual specific parameters (e.g. $L_{i\infty}$ and K_i) which where treated as unknown random nuisance parameters. For tagging data Palmer et al. (1991) considered the initial age a as missing data having a random distribution. For tag-return data Palmer et al. (1991) proposed a nonparametric approach to modelling the age distribution of tagged animals. Palmer et al. (1991) used the EM algorithm approach for estimation based on the marginal distribution of growth after integrating over the densities of the random growth parameters and a.

Wang et al. (1995) considered intrapopulation variability in L_∞, and measurement error. They used a transformation of variables approach to derive the model distribution of length-at-release and length-at-capture based on the distributions of L_∞ and A - a random variable representing age-at-release. In an example, Wang et al. (1995) used a normal distribution for L_∞, and a gamma distribution for A. In a simulation study they concluded that their procedure performed better than Fabens' method, even if the shape of the growth curve was mis-specified. Wang et al. (1995) also presented a discussion about their rationale for treating K as fixed. They concluded that in practise it is difficult to estimate σ_κ^2 with tag-return data because there are only two growth measurements per fish. They also felt that L_∞ was more important than K when extrapolating growth.

Wang and Thomas (1995) also examined the effect of intrapopulation variability in VONB growth model parameters. Their main point was that $E\{L_\infty | L(a) = l\} \neq E(L_\infty)$. The difference between these two expectations depends on a. For example, if we know that all fish were age 2 at the time of tagging, then $E\{L_\infty | L(a) = l\} = l/(1 - e^{-2k})$. This is relevant because one approach to estimation with (4) is to use the conditional distribution of the growth increment; that is, if $G = L_c - L_\tau$ then one approach to estimation is to use the conditional distribution of $G|L_\tau = l_\tau$; however, this distribution is dependent on a, and we need to know the age-at-release to estimate parameters in the standard manner. Wang and Thomas (1995) also showed using simulations that Fabens' method and the methods outlined in Sainsbury (1980) and Kirkwood and Somers (1984) produced substantially (% error>100) biased estimates of μ_∞ and κ. The biases in Fabens' estimators of λ_∞ and κ were substantially larger when both L_∞ and K were random than when only L_∞ was random.

Wang (1998) presented a simplified approach to the estimation of VONB growth parameters in which $E\{L_\infty | L(a) = l_\tau\}$ was approximated as $\mu_\infty + \beta(l_\tau - \bar{l}_\tau)$ where $\bar{l}_\tau$ is the average length-at-release and β is a parameter used to model the dependence of

$E\{L_\infty|L(a) = l_r\}$ on l_r. For example, if both L_r and L_∞ have a bivariate normal distribution then $\beta = cov(L_\infty, L_r)/Var(L_r)$. In a simulation study Wang (1998) showed that estimators of μ_∞ and κ based on the approximation to $E\{L_\infty|L(a)\}$ were much less biased than Fabens' estimators. The estimators also tended to be more efficient than those proposed by James (1991).

Another stochastic aspect of growth modelling was considered by Prajneshu and Venugopalan (1999). They objected to the fact that the VONB model predicts future growth with complete certainty. They preferred the approach where the growth rate $G'(t)$ is modelled as a stochastic process $G'(t) = \kappa\{G(\infty) - G(t)\} + K(t)$, where $K(t)$ is a zero-mean stochastic process with $Cov\{K(t_1), K(t_2)\}$ decreasing as $|t_1 - t_2|$ increases. Wang (1999) considered a similar framework, although he allowed for a more arbitrary growth rate model, in which κ was replaced by a function of covariates. Wang (1999) also considered measurement errors in lengths, and he extended the estimating equations approach of James (1991) to the stochastic growth model. Autocorrelation in errors between growth and the VONB curve was also mentioned by Millar (1992), although he explored this only in a simulation-based sensitivity analysis. Stochastic growth is another plausible mechanism that can be considered to explain the variability observed in our growth increment data. Note that some of the bias caused by ignoring intrapopulation variability in growth parameters are attenuated when the time correlation between VONB parameters is reduced (see Wang et al., 1995), so this may be important when considering variability in growth parameters.

The potential for non-random sources of variability in the growth rates of cod in 3Ps and 3KL have been suggested in the literature. Lilly (1998) documented several ancillary sources of information that suggest cod growth rates in 3Ps may vary seasonally, with lower growth rates in the winter and early spring. Millar and Myers (1990) found that 12% of the residual variation in fitting a VONB growth curve to average length-at-age data for 3Ps cod could be explained by a model that included a total biomass effect and a water temperature effect. In 3K and 3L the proportion of variation explained by these two factors was 48% and 33%, respectively. Shelton et al. (1999) reviewed the literature related to the effect of temperature on cod growth, and also studied the relationship between the area of the cold intermediate layer (CIL) and weight increments for cod in 2J3KL. They concluded that the CIL accounted for 41% of the variability in weight increments. We will not consider the influence of such exogenous factors on growth here, but we conclude from these studies that growth rates in 3Ps and 3KL may vary seasonally and annually because of, for example, changes in temperature. Models for seasonal growth rates have been proposed by Pitcher and Macdonald (1973), Cloern and Nichols (1978), and Pauly et al. (1992), among others.

4.2 Simulation study of intrapopulation variability in growth

The problem of intrapopulation variability in VONB growth parameters essentially involves how to interpret tag-return data in terms of (2). This is important if the desire is to make inferences about the growth of a non-sampled individual; however, our problem

involves reasonably predicting the length of a fish following tagging, in which case (3) may be a reasonable model even if population growth follows (2) with variability in the parameters. The biases considered in the above literature usually involve parameters, whereas what is more relevant to us is the bias in predicting the growth increment of a fish.

In this section we present a simple simulation study to assess the relevance of intrapopulation variability to the estimation of length-at-capture from a known (no measurement error) length-at-release. Our intent is to decide what method of estimation to use with our data. We simulate the biases in Fabens' estimators of λ_∞ and κ, and also assess the utility of the estimators presented in James (1991) and Wang (1998). We use a similar procedure as in Wang and Thomas (1995) to generate simulated growth data.

We generated simulated data as follows. Preliminary analyses using Fabens' method suggested that λ_∞ for our data is in the range of $115 - 140$, and κ is in the range of $0.002 - 0.005$ on a weekly scale. The steps in our simulation were:

Step 1. We generated L_∞'s from a normal distribution with mean $\mu_\infty = 130$ and a standard error of 13; that is, a 10% coefficient of variation (CV). We generated values for K from a gamma distribution with mean $\kappa = 0.102$, and a 10% CV. This value for κ is 0.002 converted to an annual scale (i.e. $\times 52$).

Step 2. We generated lengths-at-tagging using (4) and the random values for L_∞ and K from Step 1, but with no measurement errors.

Step 3. To use (4) we also needed to specify the age-at-tagging. We speculated that the ages of most fish when tagged (a) were in the range of $5 - 12$ years, and we decided to generate lengths-at-tagging using a uniform distribution for a over $5 - 12$.

Step 4. Individual lengths-at-capture were simulated using different VONB parameters than those in Step 1. These parameters were generated similarly to those in Step 1, but the new parameters were constrained to be correlated (coefficient = 0.5) with those in Step 1. As a result, our simulation has the feature that growth before and after tagging is autocorrelated, but not perfectly so.

Step 5. Random times-at-liberty (t) were drawn from a distribution based on the actual t's in our data set. This distribution is shown as a solid line in Fig. 9.

Step 6. Fish lengths at the time-of-capture were computed using the second equation in (4).

Step 7. The reported lengths-at-capture were modelled with normally distributed measurement error (CV= 10%).

The sample size in our simulation was 1000. This is less than the sample size in our data set (1578), but our simulation model is considerably more simple than the model we eventually chose for our data, so we reduce the sample size to compensate. In

future research we will perform a simulation analysis based on the chosen model. We estimate biases and standard errors using 500 simulated (replicate) data sets. VONB growth parameters, age-at-release, and age-at-capture were randomly generated in each simulation.

We study four methods of estimation. The standard one is Fabens' method, which is nonlinear least squares using (3). The second method is maximum likelihood assuming L_∞ and ε_2 are normally distributed; this method is similar to Somers and Kirkwood (1991). The third method is the estimating equations approach by James (1991). The fourth method is Wang's (1998) approach based on a linear approximation to $E(L_\infty|L(a) = l_r)$. Wang's (1988) method performed very poorly in our simulations. The reason seems to be related to confounding between his β parameter and λ_∞. We will not report on this method further. The simulated biases and standard errors for the other estimators of λ_∞ and κ are presented in Table 3. The bias in Fabens' estimator of λ_∞ is substantial. James'

Table 3. Simulation averages for 3 estimators of von Bertalanffy growth parameters (standard deviations in parantheses). Population values are $\lambda_\infty = 130$, and $\kappa = 0.104$.

Method	λ_∞	%bias	κ	%bias
Faben (1965)	156.78 (25.32)	21	0.073 (0.020)	-29
James (1991)	125.93 (68.26)	-3	0.254 (0.195)	145
Somers and Kirkwood (1998)	156.47 (24.04)	20	0.073 (0.020)	-29

(1991) method seems preferable for estimating λ_∞, whereas Fabens' method seems better for estimating κ.

Of concern to us is which method is better for predicting lengths-at-capture. To assess this we computed the bias and mean square error (mse) for estimated lengths-at-capture. We computed the average bias for 10 cm release length intervals, and for 4 time-at-liberty intervals. The number of simulated growth predictions for each length and time class are presented in Table 4a. In this table we have used the set notation $[x, y)$ which means $z \in [x, y)$ if and only if $z \geq x$ and $z < y$. The average release length is almost 75 cm. Average population growth is presented in Table 4b. Our interest is to use growth measurements to accurately predict the growth shown in Table 4b. The simulation biases using Fabens' method are presented in Table 4c. The biases are generally small compared to average growth (see Table 4b). An important issue when considering the other estimation methods is mse, which we present in Table 4d for Fabens' method. The precision of our growth predictions decreases with time-at-liberty, as expected.

We have already mentioned that the results for Wang's (1998) method were discouraging. The results for James' (1991) method were also discouraging. Non-convergence was a problem when finding the roots of his estimating equations. Over 30% of the simulations did not converge. The non-converged results are excluded from further analysis (and also Table 3). The mse's are presented in Table 5 for the converged simulations . These values

Table 4a. Number of simulated growth predictions for each length and time-at-liberty class.

	Time at liberty			
Length (cm)	[0, 0.5)	[0.5, 1.5)	[1.5, 2.5)	[2.5, 3)
[25, 35)	9	9	4	1
[35, 45)	1180	960	542	70
[45, 55)	10845	8846	5093	638
[55, 65)	25428	20490	12070	1401
[65, 75)	32314	26394	15303	1765
[75, 85)	32916	26567	15734	1857
[85, 95)	23249	18816	10885	1299
[95, 105)	9655	7890	4599	576
[105, 115)	2147	1718	1015	130
[115, 125)	232	201	115	9
[125, 135)	10	11	5	1

Table 4b. Average simulated population growth for each length and time-at-liberty class.

	Time at liberty			
Length (cm)	[0, 0.5)	[0.5, 1.5)	[1.5, 2.5)	[2.5, 3)
[25, 35)	1.36	7.29	14.97	14.66
[35, 45)	1.45	7.17	12.74	17.32
[45, 55)	1.45	7.00	12.50	16.87
[55, 65)	1.35	6.53	11.64	15.69
[65, 75)	1.18	5.74	10.23	13.78
[75, 85)	1.02	4.97	8.81	11.88
[85, 95)	0.89	4.30	7.68	10.43
[95, 105)	0.78	3.80	6.73	9.05
[105, 115)	0.68	3.32	5.96	7.93
[115, 125)	0.61	2.87	5.09	6.25
[125, 135)	0.43	2.40	4.96	3.88

Table 4c. Simulated biases in Faben's estimator of growth. Biases are computed for each length and time-at-liberty class.

	Time at liberty			
Length (cm)	[0, 0.5)	[0.5, 1.5)	[1.5, 2.5)	[2.5, 3)
[25, 35)	0.25	1.39	1.83	3.92
[35, 45)	0.08	0.53	1.03	1.42
[45, 55)	-0.02	-0.01	0.11	0.30
[55, 65)	-0.05	-0.19	-0.20	-0.09
[65, 75)	-0.03	-0.08	0.00	0.13
[75, 85)	-0.01	0.03	0.16	0.34
[85, 95)	-0.02	-0.01	0.07	0.13
[95, 105)	-0.04	-0.17	-0.18	-0.09
[105, 115)	-0.08	-0.36	-0.57	-0.61
[115, 125)	-0.13	-0.56	-0.96	-0.50
[125, 135)	-0.10	-1.10	-1.89	1.70

Table 4d. Simulated mse in Faben's estimator of growth. Mse's are computed for each length and time-at-liberty class.

	Time at liberty			
Length (cm)	[0, 0.5)	[0.5, 1.5)	[1.5, 2.5)	[2.5, 3)
[25, 35)	0.16	4.49	6.09	15.51
[35, 45)	0.07	1.31	3.84	6.71
[45, 55)	0.06	1.00	2.79	5.14
[55, 65)	0.06	1.10	3.06	5.05
[65, 75)	0.06	1.04	3.03	5.38
[75, 85)	0.05	0.92	2.77	4.96
[85, 95)	0.05	0.85	2.62	4.58
[95, 105)	0.05	0.95	2.72	4.76
[105, 115)	0.07	1.25	3.88	6.69
[115, 125)	0.10	1.70	4.31	10.78
[125, 135)	0.07	2.48	6.49	6.29

Table 5. Simulated mse in Jame's (1991) estimator of growth. Mse's are computed for each length and time-at-liberty class.

	Time at liberty			
Length (cm)	[0, 0.5)	[0.5, 1.5)	[1.5, 2.5)	[2.5, 3)
[25, 35)	2.10	148.40	148.97	644.22
[35, 45)	4.34	56.28	97.57	123.91
[45, 55)	2.42	25.64	48.51	55.50
[55, 65)	1.10	10.45	18.15	19.95
[65, 75)	0.30	2.77	4.96	6.52
[75, 85)	0.08	1.67	5.94	12.41
[85, 95)	0.43	7.80	22.20	37.76
[95, 105)	1.47	22.22	55.14	82.14
[105, 115)	2.92	41.75	104.37	140.77
[115, 125)	4.09	63.35	213.39	189.36
[125, 135)	4.66	57.55	739.89	270.40

greatly exceed those for Fabens' method (see Table 4d), and suggest that James' (1991) method is not suitable for our data. This is probably due to the short times-at-liberty for many of the tag-returns (see Fig. 9).

The results in Table 3 suggest that the weighted least-squares approach similar to Somers and Kirkwood (1991) produces similar results as Fabens' method in our simulation. The mse's are presented in Table 6. These values are very similar to those in Table 4d, and do not suggest that the weighted least-squares approach offers much improved estimators of VONB growth parameters. The reason for the similarity is that error variance component was usually estimated to be much greater than VONB variance component (median ratio was 18.6). In this case the variance model is approximately constant, and one expects the estimates to be similar to un-weighted least-squares estimates.

Our conclusion from the simulation exercise is that Fabens' method is better than the methods of Wang (1998) or James (1991) to estimate parameters for our tagging data. Wang's (1998) and James' (1991) approaches did not work well possibly because of the relatively short times-at-liberty (see Fig. 9) and because we allowed pre- and post-release VONB growth parameters to vary somewhat (i.e. 0.5 correlation). Our results are preliminary, and further investigation is required; however, for the current assessment we will use Fabens' approach for estimation. For our final model we will also assess the impact of intrapopulation variability in (3) using the weighted least-squares approach.

Table 6. Simulated mse in Somers and Kirkwood's (1991) estimator of growth. Mse's are computed for each length and time-at-liberty class.

	Time at liberty			
Length (cm)	[0, 0.5)	[0.5, 1.5)	[1.5, 2.5)	[2.5, 3)
[25, 35)	0.17	4.51	4.53	14.00
[35, 45)	0.07	1.31	3.84	7.13
[45, 55)	0.06	1.01	2.81	5.16
[55, 65)	0.06	1.10	3.06	5.07
[65, 75)	0.06	1.04	3.03	5.41
[75, 85)	0.05	0.93	2.78	4.98
[85, 95)	0.05	0.85	2.62	4.60
[95, 105)	0.05	0.94	2.74	4.75
[105, 115)	0.07	1.23	3.80	6.85
[115, 125)	0.10	1.61	4.30	10.64
[125, 135)	0.07	2.66	5.88	5.77

5 Von Bertalanffy growth model with regional growth rates

In this section we investigate whether growth rates vary for the three regions we identified in **Section 2**. We estimate the parameters of (3) using tags from fish that were released and returned in the same region. This is the same data that is shown in Figs. 2-4. Recall from the analyses in **Section 3** (also see Figs. 5-6) that we have good reason to suspect that the growth increment measurements are biased, and that the bias is a function of length-at-capture. We also suspect that the bias function changes annually. Fortuitously we can estimate this bias, because fish caught within a short time following release should not grow much, and the growth increments reported for such fish can be used to estimate bias. We use a parametric model for bias, which we add to (3) when estimating growth rates.

The bias function we use is

$$b(l;\beta_o,\beta_1,\beta_2) = \beta_o + \frac{\beta_1 \exp(l-\beta_2)}{1+\exp(l-\beta_2)}.$$

If $l_{\min}-\beta_2 << 0$ and $l_{\max}-\beta_2 >> 0$ then $b(l;\beta_o,\beta_1,\beta_2)$ ranges from β_o to $\beta_o+\beta_1$ with an inflection at β_2. This is basically the behavior we observe in Fig. 6. We estimate β_o and β_1 separately each year. Preliminary analysis did not suggest that β_2 varied significantly from year to year. The bias is a function of the length of fish at capture, so we must use (3) to model l. Hence, our model for the random variable G_y representing the growth

increment of a fish reported in year y is

$$E(G_y) = b\left\{l_r + (\lambda_{i\infty} - l_r)(1 - e^{-\kappa_i t}); \beta_{y,0}, \beta_{y,1}, \beta_2\right\} + (\lambda_{i\infty} - l_r)(1 - e^{-\kappa_i t}).$$

There are 13 unknown parameters to estimate in this model: $\beta_{y,o}$, $\beta_{y,1}$ for $y = 1997, ..., 1999$, β_2, and $\lambda_{i\infty}$, κ_i for the three regions i. We assume that the bias is the same in each region, but varies annually.

We estimate the bias and VONB growth parameters using nonlinear least-squares. To make the assessment of the regional differences in VONB growth parameters easier we actually estimate λ_∞ and κ for region 1 (i.e. $\lambda_{1\infty}$ and κ_1), and the differences in λ_∞ and κ between regions 2 and 3, and region 1; that is, $\lambda_{i\infty} - \lambda_{1\infty}$ and $\kappa_i - \kappa_1$, for $i = 2$ and 3. If the differences are significant then we conclude that the population parameter values are different. This is the procedure advocated by Cerrato (1990). We do the same for the bias parameters, except for β_2. Estimates and some inference results are presented in Table 7. The β_o parameters in 1997 and 1999 are significantly different (see P-value

Table 7. Estimation results for the regional von Bertalanffy analysis of cod growth increments (cm).

Parameter	Estimate	Approx. Std Err	T Ratio	Approx. Prob>|t|
$\lambda_{1\infty}$	118.15	14.13	8.36	<0.01
$\lambda_{2\infty} - \lambda_{1\infty}$	-29.56	37.94	-0.78	0.44
$\lambda_{3\infty} - \lambda_{1\infty}$	-8.23	39.26	-0.21	0.83
κ_1	0.0023	0.0006	3.78	<0.01
$\kappa_2 - \kappa_1$	0.0034	0.0080	0.42	0.67
$\kappa_3 - \kappa_1$	0.00025	0.0022	0.11	0.91
$\beta_{1999,0}$	-0.087	0.572	-0.15	0.88
$\beta_{1999,1}$	-4.68	0.641	-7.30	<0.01
β_2	64.10	0.928	69.1	<0.01
$\beta_{1997,0} - \beta_{1999,0}$	-1.97	0.966	-2.04	0.04
$\beta_{1997,1} - \beta_{1999,1}$	0.69	1.048	0.66	0.51
$\beta_{1998,0} - \beta_{1999,0}$	-1.31	0.810	-1.61	0.11
$\beta_{1998,1} - \beta_{1999,1}$	2.30	0.980	2.35	0.02

for $\beta_{1997,0} - \beta_{1999,0}$ in Table 7), and β_1 in 1998 and 1999 are also significantly different. The differences in VONB growth parameters between regions 2 and 3 and region 1 are not significant.

While the VONB parameters for regions 2 and 3 are not significantly different from those for region 1, they could be different from each other. We use an F statistic based on a likelihood-ratio test (see Seber and Wild, 1989) to investigate whether there are any differences among the growth parameters for the three regions. First we fit a model with these parameters constrained to be equal for all regions ("no region" model). These results are presented in Table 8. The SSE for the "no region" model is 79150.72, while

Table 8. Estimation results for the von Bertalanffy analysis of cod growth increments (cm).

Parameter	Estimate	Approx. Std Err	T Ratio	Approx. Prob>|t|
λ_∞	116.12	12.893	9.01	<0.01
κ	0.0023	0.0006	4.01	<0.01
$\beta_{1999,0}$	-0.055	0.568	-0.10	0.923
$\beta_{1999,1}$	-4.692	0.630	-7.45	<0.01
β_2	63.927	0.881	72.54	<0.01
$\beta_{1997,0} - \beta_{1999,0}$	-2.011	0.962	-2.09	0.04
$\beta_{1997,1} - \beta_{1999,1}$	0.778	1.037	0.75	0.45
$\beta_{1998,0} - \beta_{1999,0}$	-1.350	0.808	-1.67	0.09
$\beta_{1998,1} - \beta_{1999,1}$	2.341	0.968	2.42	0.02

the SSE for the regional model is 79090.74. The test statistic for regional growth rates is $F_{obs} = 0.3$, and the p-value for this test statistic is $\Pr(F_{4,1565} > F_{obs}) = 0.88$, so these data do not suggest that growth rates are different among the three regions. As in the regional analysis, the annual biases are significantly different in the "no region" model.

The next step is to examine whether growth rates vary annually or seasonally. When doing this we assume growth rates are constant throughout 3Ps and 3KL. A model combining regional and annual/seasonal growth rates contains too many parameters for us to reasonably estimate because of the small number of tag-returns in 3KL. This is the same as assuming there are no annual-regional interactions.

6 Von Bertalanffy growth model with annual growth rates

We will first develop a VONB growth model in which the growth rates can vary annually, much in line with Millar and Myers (1990). Equation (3) implies that the growth rates are the same for fish released at the same time, apart from a proportionality constant depending on l_τ. We will retain this feature in our model. Note that fish of different length may occupy different habitats and experience different annual fluctuations in length (i.e. length-year interaction); however, we will not explore this here. We model annual variations in growth rates by modifying the κ parameter.

The VONB growth equation is the solution (see Bhattacharya, 1966) of the differential equation $\dot{L}(t) = \kappa\{\lambda_\infty - L(t)\}$, where $\dot{L}(t) = dL(t)/dt$. The modification we propose is $\dot{L}(t) = \dot{K}(t)\{\lambda_\infty - L(t)\}$. The solution to this differential equation using the boundary condition $L(0) = 0$ is

$$L(t) = \lambda_\infty \left\{1 - e^{-K(t)}\right\}. \tag{5}$$

If $\dot{K}(t) = \kappa$ is constant then $K(t) = \kappa t$ and $L(t)$ is given by (2). For annually varying growth rates we use $\dot{K}(t) = \kappa_y$, where κ_y is constant for year y. The solution to this VONB differential equation requires some additional notation. Let t_x denote the release time for tagging experiment x. Let t denote the capture time. Both t and t_x are in weeks from the beginning of the year. The VONB annual growth equation is given by (5), with

$$K(t) = \begin{cases} \kappa_y(t - t_x), & \text{if } t \in y,\ t_x \in y, \\ \kappa_y(52 - t_x) + \kappa_{y+1}t, & \text{if } t_x \in y,\ t \in y+1, \\ \kappa_y(52 - t_x) + 52\kappa_{y+1} + \kappa_{y+2}t, & \text{if } t_x \in y,\ t \in y+2. \end{cases} \tag{6}$$

We use the same procedure as before, and estimate κ_{1999} and the differences $\kappa_{1997} - \kappa_{1999}$ and $\kappa_{1998} - \kappa_{1999}$. Estimates and some inference results are presented in Table 9. There

Table 9. Estimation results for the annual von Bertalanffy analysis of cod growth increments (cm).

Parameter	Estimate	Approx. Std Err	T Ratio	Approx. Prob>|t|
λ_{co}	115.16	12.34	9.34	<0.01
$\kappa_{1997} - \kappa_{1999}$	0.00008	0.00059	0.14	0.89
$\kappa_{1998} - \kappa_{1999}$	-0.0015	0.00096	-1.56	0.12
κ_{1999}	0.0031	0.00094	3.33	<0.01
$\beta_{1999,0}$	-0.320	0.621	-0.52	0.61
$\beta_{1999,1}$	-4.551	0.640	-7.12	<0.01
β_2	64.007	0.909	70.38	<0.01
$\beta_{1997,0} - \beta_{1999,0}$	-2.138	1.006	-2.13	0.03
$\beta_{1997,1} - \beta_{1999,1}$	0.849	1.037	0.82	0.41
$\beta_{1998,0} - \beta_{1999,0}$	-0.492	0.985	-0.50	0.62
$\beta_{1998,1} - \beta_{1999,1}$	1.979	0.969	2.04	0.04

is only weak evidence that the growth rates vary annually; that is, the P-value is 0.12 for the $\kappa_{1998} - \kappa_{1999}$ term. The bias functions are plotted in Fig. 10. They can be compared to the nonparametric estimates in Fig. 6. The bias increases with fish length, and is largest in 1997. Fig. 6 suggests this as well. The growth rates estimated from this model are shown in Fig 11. In this figure weeks are cumulative since 1997. We have plotted estimated growth rates for 36 hypothetical fish to demonstrate the model. For example, a 40 cm fish released in week 20 (end of May, 1997) is estimated to grow a little over 21 cm by week 150 (mid Nov, 1999), whereas a 90 cm fish released at the same time is estimated to grow only 7 cm by week 150. This is exactly the information we require to estimate the length-at-capture for the tag-returns.

We assess the validity of the model using residual plots. We examined many residual diagnostics, but to save space we present only the residual plot that suggests the largest departure in our model assumptions. In Fig. 12 we plot weekly averaged standardized residuals. The kernel regression smoother bandwidth we use minimizes the cross-validation

statistic (see Härdle, 1991). Particularly in 1998 and 1999, the smoother highlights the seasonal pattern in the residuals; that is, the annual model tends to over-estimate growth in the first part of the year (negative residuals), and under-estimate growth in the second part of the year (positive residuals). Residual plots versus release length, time-at-liberty, and predicted value did not suggest any further deviations in model assumptions.

7 Von Bertalanffy growth model with annual/seasonal growth rates

We introduce a simple modification to allow for seasonal growth. We model a period of no growth followed by a growth period. Pitcher and Macdonald (1973) referred to this as switched growth. We estimate the break-points between the growth and no growth periods (similar to β_2 in the bias model). There are three additional parameters to estimate for our data, which are the break-points in growth during 1997-1999.

The growth model involves a simple modification of (6). Let $x_+ = \max(x, 0)$, and let θ_y denote the growth break-point in year y, measured from weeks since the beginning of the year. The seasonal model for $K(t)$ is

$$K(t) = \begin{cases} \kappa_y \{(t-\theta_y)_+ - (t_x-\theta_y)_+\}, & \text{if } t \in y,\ t_x \in y, \\ \kappa_y \{52-\theta_y-(t_x-\theta_y)_+\} + \kappa_{y+1}(t-\theta_{y+1})_+, & \text{if } t_x \in y,\ t \in y+1, \\ \kappa_y \{52-\theta_y-(t_x-\theta_y)_+\} + \kappa_{y+1}(52-\theta_{y+1}) & \\ \quad + \kappa_{y+2}(t-\theta_{y+2})_+, & \text{if } t_x \in y,\ t \in y+2. \end{cases} \tag{7}$$

To assess annual differences in θ_y's we estimate θ_{1999} and the differences $\theta_{1997} - \theta_{1999}$ and $\theta_{1998} - \theta_{1999}$. Estimation results are presented in Table 10. The SSE for the annual model is 78960.48, and the SSE for the seasonal model is 76744.34. Note that the annual model is nested within the seasonal model, because they are the same if all $\theta = 0$. The F statistic for the seasonal model is $F_{obs} = 15.05$, with a p-value < 0.001 obtained from $\Pr(F_{3,1564} > F_{obs})$. This is a significant amount of "explained" variability compared to the annual model.

The gradients for the θ_y parameters are fairly large, and this causes problems when computing the approximate standard errors, so it is difficult to interpret the significance of the differences in growth break-points. The F-test is a better approach in this situation. The p-value for the overall test that θ_y's differ is 0.38, and this suggests the differences in break-points are not significant. Note that the usual procedure following this is to test whether any pairs of break-points are different; however, we will not pursue this. The results suggest that growth starts around week 30 (late July), but could occur a month earlier.

The estimate of λ_{∞} is considerably larger than in Table 7. To some extent length-dependent bias is confounded with λ_{∞}. To assess whether the differences in estimates of λ_{∞} might be related to differences in estimates of the bias function, we plot the estimated bias function from the seasonal model in Fig. 13, and compare it with Fig. 10. The bias functions are almost identical for 1999, and differ in magnitude by no more than 1 cm

Table 10. Estimation results for the seasonal von Bertalanffy analysis of cod growth increments (cm).

Parameter	Estimate	Approx. Std Err	T Ratio	Approx. Prob>|t|
λ_∞	137.66	17.43	7.90	<0.01
$\kappa_{1997} - \kappa_{1999}$	-0.0026	0.0010	-2.14	0.03
$\kappa_{1998} - \kappa_{1999}$	-0.0031	0.0012	-2.53	0.01
κ_{1999}	0.0066	0.0015	3.64	<0.01
$\theta_{1997} - \theta_{1999}$	-5.901	3.093	-1.91	0.06
$\theta_{1998} - \theta_{1999}$	-4.091	4.641	-0.88	0.38
θ_{1999}	30.90	1.817	17.01	<0.01
$\beta_{1999,0}$	-0.218	0.377	-0.58	0.56
$\beta_{1999,1}$	-4.631	0.426	-10.88	<0.01
β_2	64.89	0.568	114.28	<0.01
$\beta_{1997,0} - \beta_{1999,0}$	-1.485	0.702	-2.11	0.03
$\beta_{1997,1} - \beta_{1999,1}$	0.085	0.719	0.12	0.91
$\beta_{1998,0} - \beta_{1999,0}$	-0.682	0.707	-0.97	0.33
$\beta_{1998,1} - \beta_{1999,1}$	1.712	0.749	2.29	0.02

in 1997 and 1998. It seems unlikely that this could cause the differences in estimates of λ_∞'s. The estimators for λ_∞ and κ_y tend to be highly correlated so the growth curves may be similar, even if the parameter estimates are not. Growth estimates from the seasonal model are presented in Fig. 14. On a broad scale these estimates are similar to those in Fig. 11, but substantial deviations do occur. For example, compare the growth at week 150 for an 80 or 90 cm fish released in week 20. The seasonal model estimates 3-4 cm more growth than the annual model. These are interesting differences that are worthy of further investigation.

Weekly-averaged standardized residuals are shown in Fig. 15. Autocorrelation is still evident in the residuals, but to a lesser extent than in Fig. 12. Further refinement of the seasonal model may substantially improve model fit, and this will be an area for future research.

7.1 Intrapopulation variability

In **Section 5** we concluded that Fabens' method of estimation was the best approach for our tagging data, but that weighted least-squares similar to Somers and Kirkwood (1991) worked almost as well. In this section we use the weighted least squares approach to test for the potential sensitivity of our results to intrapopulation variability. The variance model we use is based on the assumption that λ_∞ in (3) is random, and that there is measurement error in the lengths-at-capture. The variance model appropriate for these assumptions is $Var[G(t)] = \sigma_\epsilon^2 + \sigma_\infty^2 \left\{1 - e^{-K(t)}\right\}^2$. We estimated (5) using

maximum likelihood assuming growth measurements were normally distributed with this variance function. Estimation results are presented in Table 11. The σ^2_∞ parameter

Table 11. Estimation results for the seasonal von Bertalanffy analysis of cod growth increments (cm), assuming intrapopulation variability in L_∞'s.

Parameter	Estimate	Approx. Std Err	T Ratio	Approx. Prob>|t|
λ_∞	139.05	23.40	5.94	<0.01
$\kappa_{1997} - \kappa_{1999}$	-0.0012	0.0009	-1.41	0.16
$\kappa_{1998} - \kappa_{1999}$	-0.0018	0.0011	-1.59	0.11
κ_{1999}	0.0046	0.0015	3.05	<0.01
$\theta_{1997} - \theta_{1999}$	-4.649	3.481	-1.34	0.18
$\theta_{1998} - \theta_{1999}$	1.459	5.086	-0.29	0.77
θ_{1999}	29.65	2.114	14.02	<0.01
$\beta_{1999,0}$	-0.233	0.377	-0.62	0.54
$\beta_{1999,1}$	-4.560	0.435	-10.50	<0.01
β_2	64.89	0.607	106.99	<0.01
$\beta_{1997,0} - \beta_{1999,0}$	-1.509	0.643	-2.35	0.02
$\beta_{1997,1} - \beta_{1999,1}$	0.0887	0.6705	0.13	0.89
$\beta_{1998,0} - \beta_{1999,0}$	-0.6133	0.6775	-0.91	0.37
$\beta_{1998,1} - \beta_{1999,1}$	1.655	0.762	2.17	0.03
σ^2_e	42.85	1.454	29.47	<0.01
σ^2_∞	826.4	475.6	1.74	0.08

estimate is large; however, one must remember that in $Var[G(t)]$ this term is multiplied by $\left\{1 - e^{-K(t)}\right\}^2$ which is very small. The likelihood-ratio test statistic for $H_o : \sigma^2_\infty = 0$ is 22.37, and the chi-square approximate p-value for this statistic is < 0.0001. This suggests that σ^2_∞ is significantly different from zero. The estimate of λ_∞ is smaller than in Table 10.

The estimated bias functions are shown in Fig. 16. The bias functions are more similar to the annual model (Fig. 10) that the seasonal model with no intrapopulation variation in growth (Fig. 13). Estimated growth curves are shown in Fig. 17. Growth in this figure tends to lie between the growth suggested in Figs. 11 and 14. For completeness we present weekly-averaged standardized residual plots in Fig. 18; they appear similar to those in Fig. 15.

We also examined length-stratified plots of standardized residuals versus time-at-liberty, which are presented in Fig. 19. While the residual variation in these plots is large, they do not suggest any systematic mis-specification of our model. Another aspect of the model is the potential for a nonlinear relationship between length-at-release and growth. This could be caused by age-at-length effects not included in our model. To address this we plotted residuals versus length-at-release for each release year. These

plots are presented in Fig. 20. There is some evidence of a relationship between residual and length. Growth tended to be under-estimated for large fish in 1997-1998, and over-estimated for large fish in 1999. This could indicate nonlinearity in the length component of (3) that is possibly related to different age-distributions in 1997-1999 for these large fish. It could also be that there is confounding between length-effects and season-effects not captured by our simplistic switched growth model, so we will not explore length-effects further until we refine our seasonal growth model. There is also the problem that nonlinearity in growth rates and length will be, to some extent, confounded with the relationship between bias and length.

Our final residual analysis is useful for assessing our assumption about the variance in reported growth. It is often observed in fisheries that the error variability increases with the model mean. A common diagnostic to assess this is to plot standardized residuals versus the predicted value of the observation. If our stochastic assumptions are correct then the plot should resemble a "shot-gun blast". This is exactly what we see in Fig. 21, and we conclude that our error assumptions seem reasonable. Some of the types of heterogeneity suggested in the literature would not be obvious in Fig. 21 however, and this deserves further attention in future research.

8 Discussion

The seasonal growth model we have developed is useful for predicting the length of a fish for times-at-liberty up to almost three years, based on a known initial length. Without further assumptions the growth rates are only applicable to the tagged fish used in our analyses. We wish to apply the growth rates to all the tagged fish released in 3Ps and 3KL during 1997-1999. To do so we must assume that the age-at-length distributions for all of the tagged fish are the same as the age-at-length distributions for the tagged fish in our study. This is probably not correct because of the highly length selective exploitation that occurs using gillnets. In conjunction with population variability in growth rates, length selective exploitation may mean that at different times we exploit the slower, or faster, growing components of the population. The problem will be attenuated when the tagged fish cover a wide range of lengths; however, the problem will still exist. Future research is required that focuses on the impact of gear selectivity on estimates of growth rates, and methods for dealing with this problem.

The same problem exists when extrapolating the growth rates in this study to the total populations of cod in 3Ps and 3KL during 1997-1999. For this extrapolation there may be more difficulty, because the method of capturing tagged fish becomes important. One assumption necessary for this extrapolation is that the age-at-length distributions for the entire population is the same as the age-at-length distribution caught for tagging.

Our analyses indicate that there is considerable room for improvement in the quality of the growth data from the tagging program. The large number of recaptures with negative growth increments and large variation in growth increments even for short times-at-liberty indicates that fishermen and other individuals returning tags must be better educated

in the importance of measuring and reporting recapture lengths accurately. They also need to be encouraged to routinely write down recapture information immediately after a tagged fish is caught and to refrain from guessing lengths at some later date instead of reporting them as unknown. Many individuals retain their tags until the end of the fishing season and send them in all at once. This sometimes results in poor quality recapture information, such as a broad time interval during which tagged fish were caught rather than a specific date for each tag, a broad recapture area rather than an exact location, as well as inaccurate recapture lengths.

More can also be done to improve the growth model. In reality growth will vary more smoothly than the switched growth seasonal model; however, it is a useful first approximation. A likely problem with our seasonal model is that $\dot{K}(t)$ is not allowed to smoothly increase and decrease. A more reasonable model might have $\dot{K}(t)$ increasing to a maximum at some point in the year, and then declining again. Both Pitcher and Macdonald (1972) and Cloern and Nichols (1978) presented parametric models of this type; however, adapting their approaches when growth rates vary annually presents additional challenges which we do not pursue here. Also worth mentioning here is the nonparametric monotone regression-spline approach to modelling human growth by Ramsay (1998,1999), and techniques by Heckman and Ramsay (1999). We can use these methods to nonparametrically model $K(t)$ as a monotone and possibly periodic increasing function of t. This will be another focus of future research.

9 Acknowledgments

We thank the sentinel and commercial fishers and staff of the Fisheries Evaluation, Gadoids, and Commercial Sampling Sections of DFO Science for conducting the tagging experiments and graduate students working under the Chair of Fisheries Conservation, Memorial University for tagging many of the Placentia Bay cod in 1997; C. George, D. Porter, S. Moulton, P. Upward and S. Chipman also collated the release and recapture information. We also gratefully acknowledge the assistance of Fisheries Officers and Observers in implementing the tagging program, and thank the numerous fishers and plant workers for returning tags and recapture information. Dr. J. Hutchings, Dalhousie University, kindly provided useful comments on an earlier version of this manuscript.

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10 Appendix: Figures

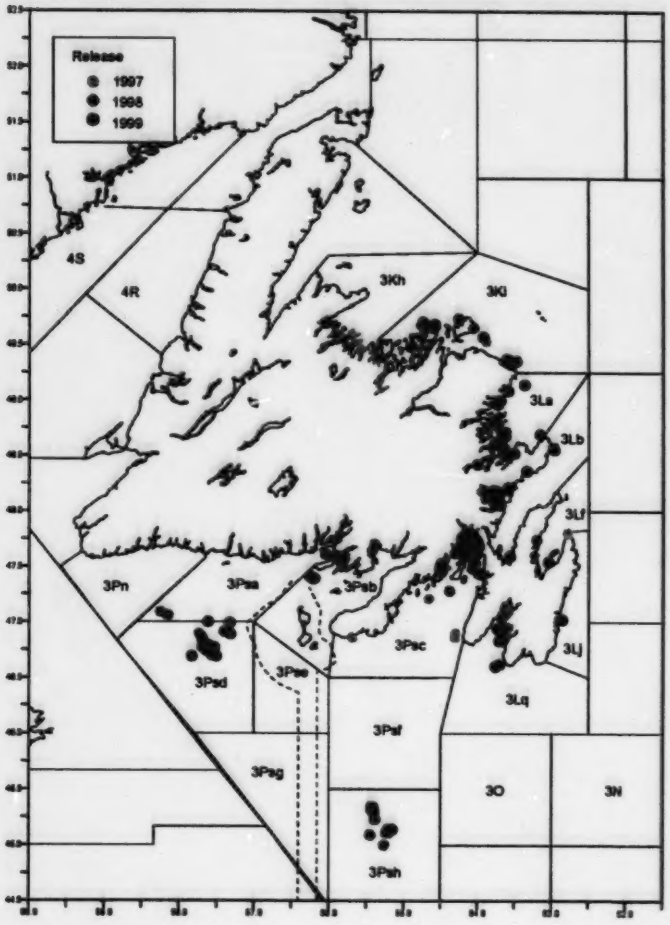

Figure 1: Map of Newfoundland showing the locations of tagging experiments during 1997-1999. NAFO subdivisions are delineated with solid lines.

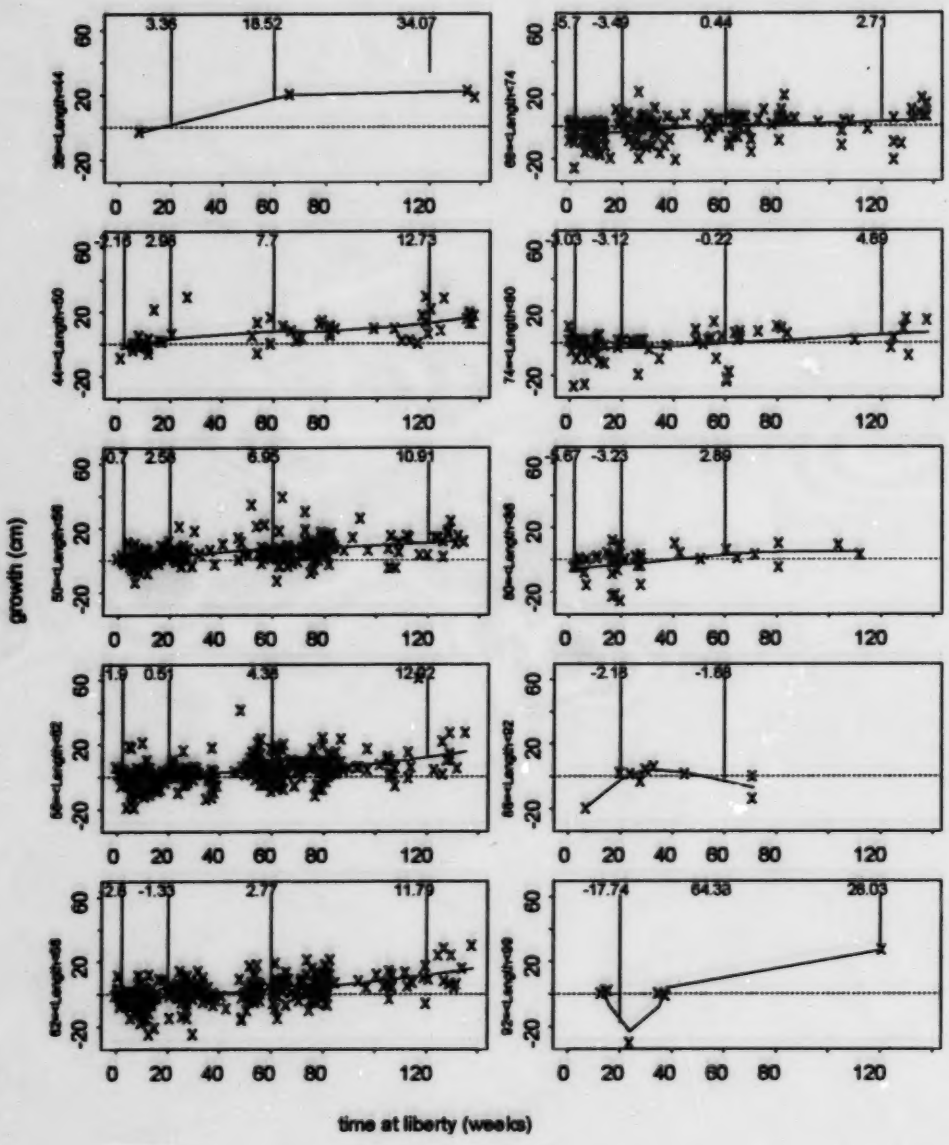

Figure 2: Reported growth of cod in 3PS from tagging data. The solid line marks a local linear smooth of the data. The numbers are the smoother predicted growth at 2, 20, 60, and 120 weeks following release.

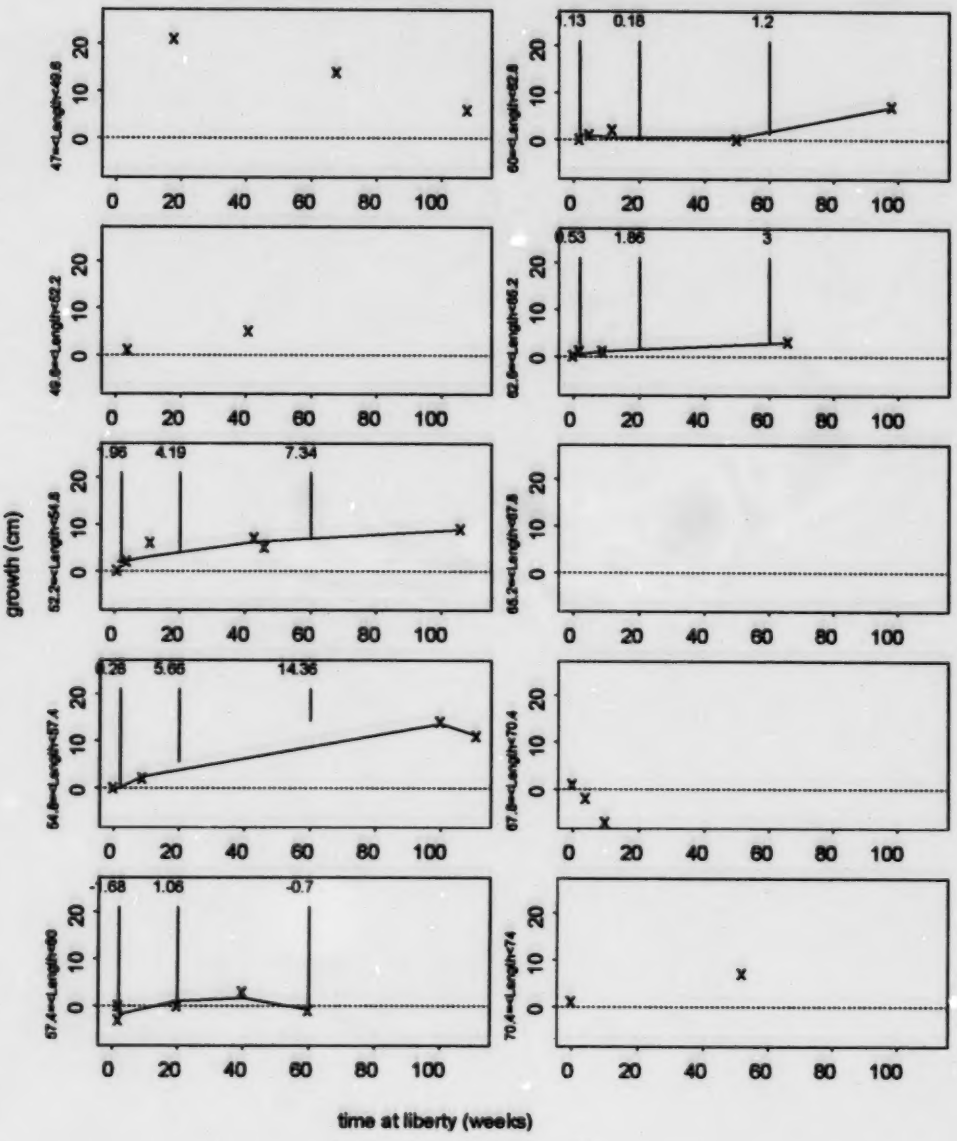

Figure 3: Reported growth of cod in southern 3L from tagging data. The solid line marks a local linear smooth of the data. The numbers are the smoother predicted growth at 2, 20, 60, and 120 weeks following release.

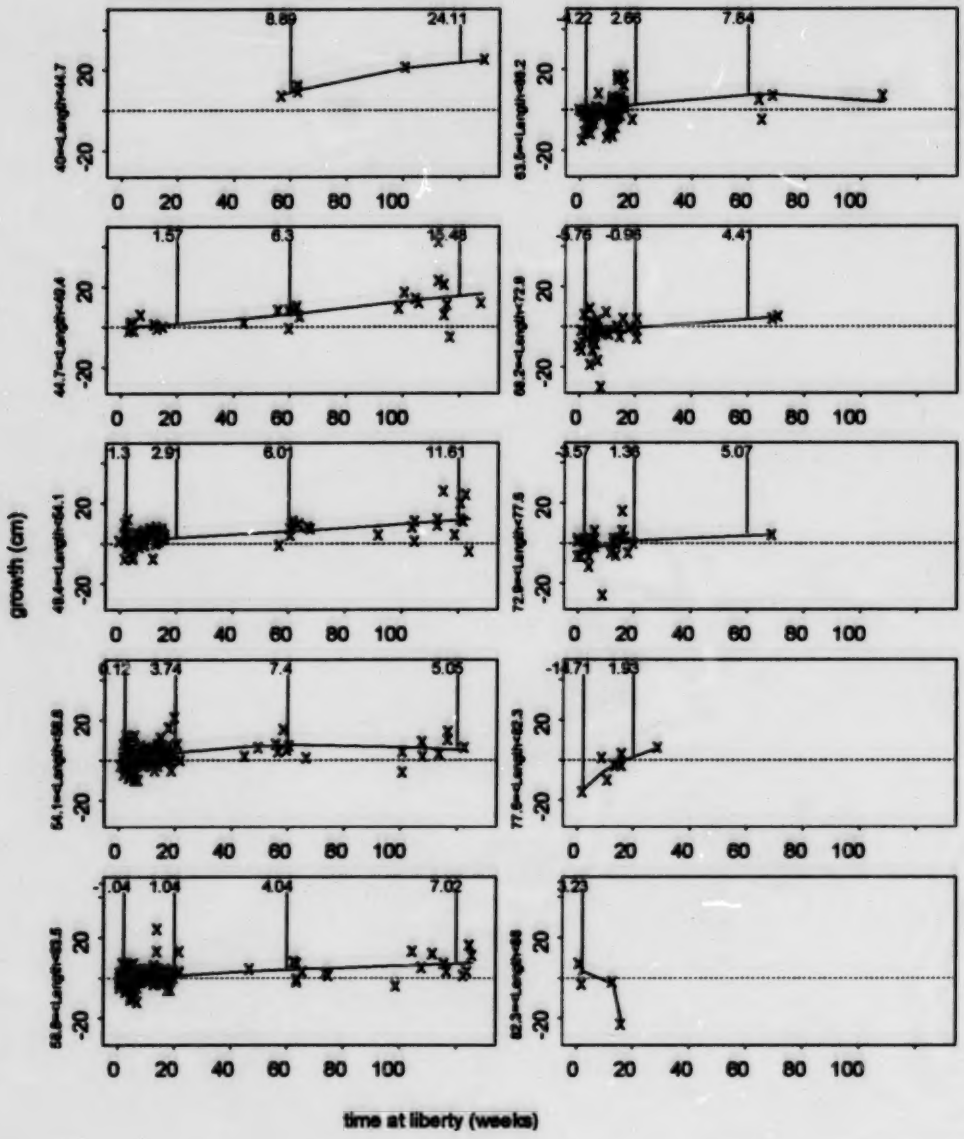

Figure 4: Reported growth of cod in northern 3L and 3K from tagging data. The solid line marks a local linear smooth of the data. The numbers are the smoother predicted growth at 2, 20, 60, and 120 weeks following release.

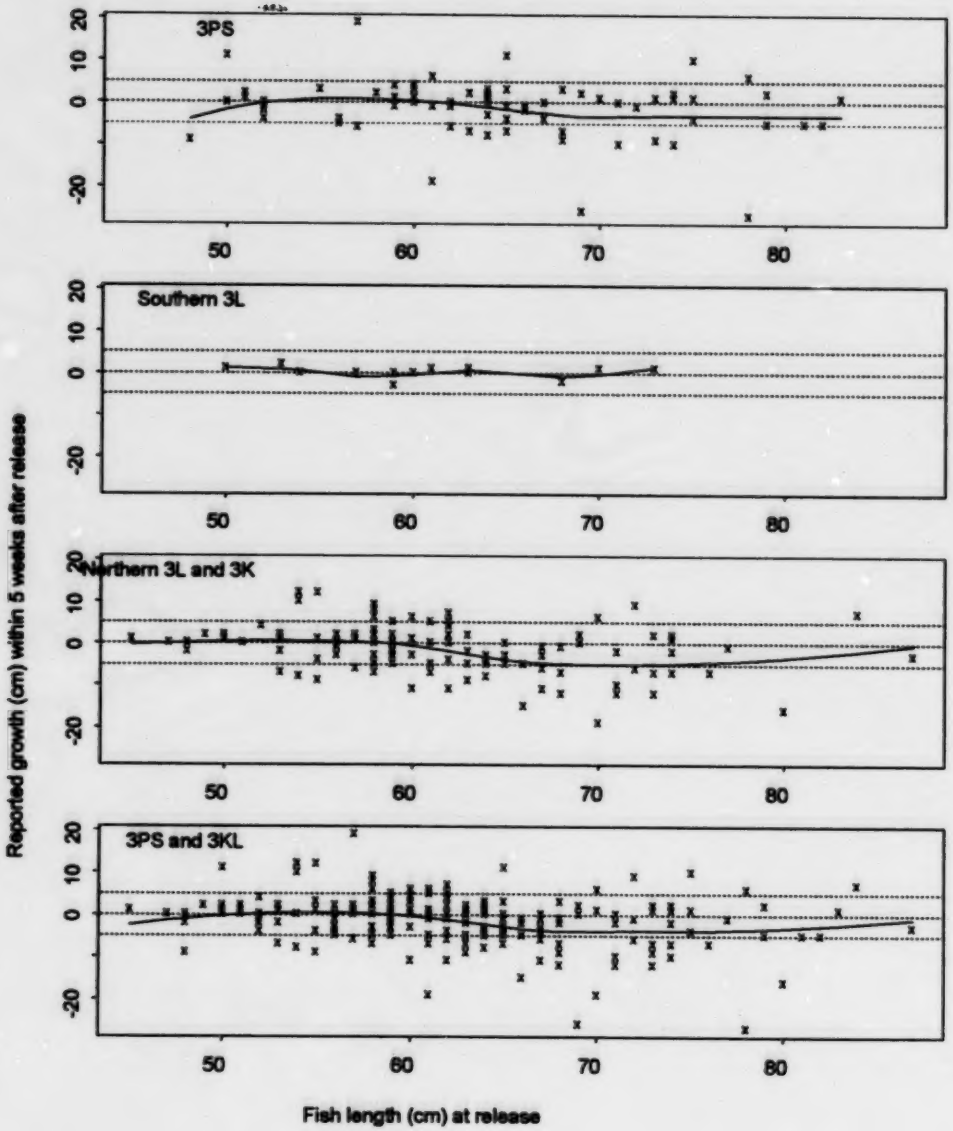

Figure 5: Bias in growth increments reported by the commercial fisheries in 3PS and 3KL during 1997-1999. Each panel represents a region, which is listed in the top left hand corner of a panel. The solid line marks a local linear smooth of the data. The dotted lines mark the -5, 0, and 5 cm growth increments.

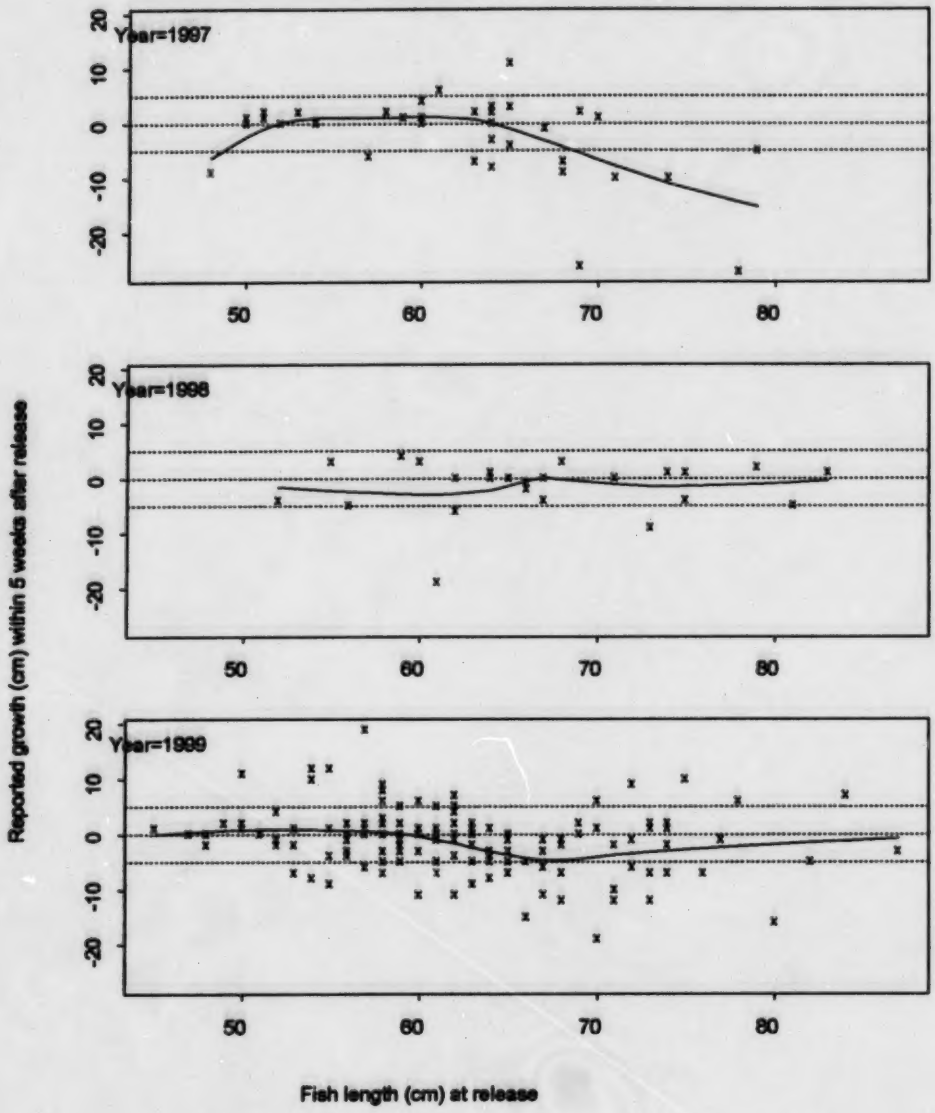

Figure 6: Bias in growth increments reported by the commercial fisheries in 3PS and 3KL during 1997-1999, versus length. Each panel represents a year. The solid line marks a local linear smooth of the data. The dotted lines mark the -5, 0, and 5 cm growth increments.

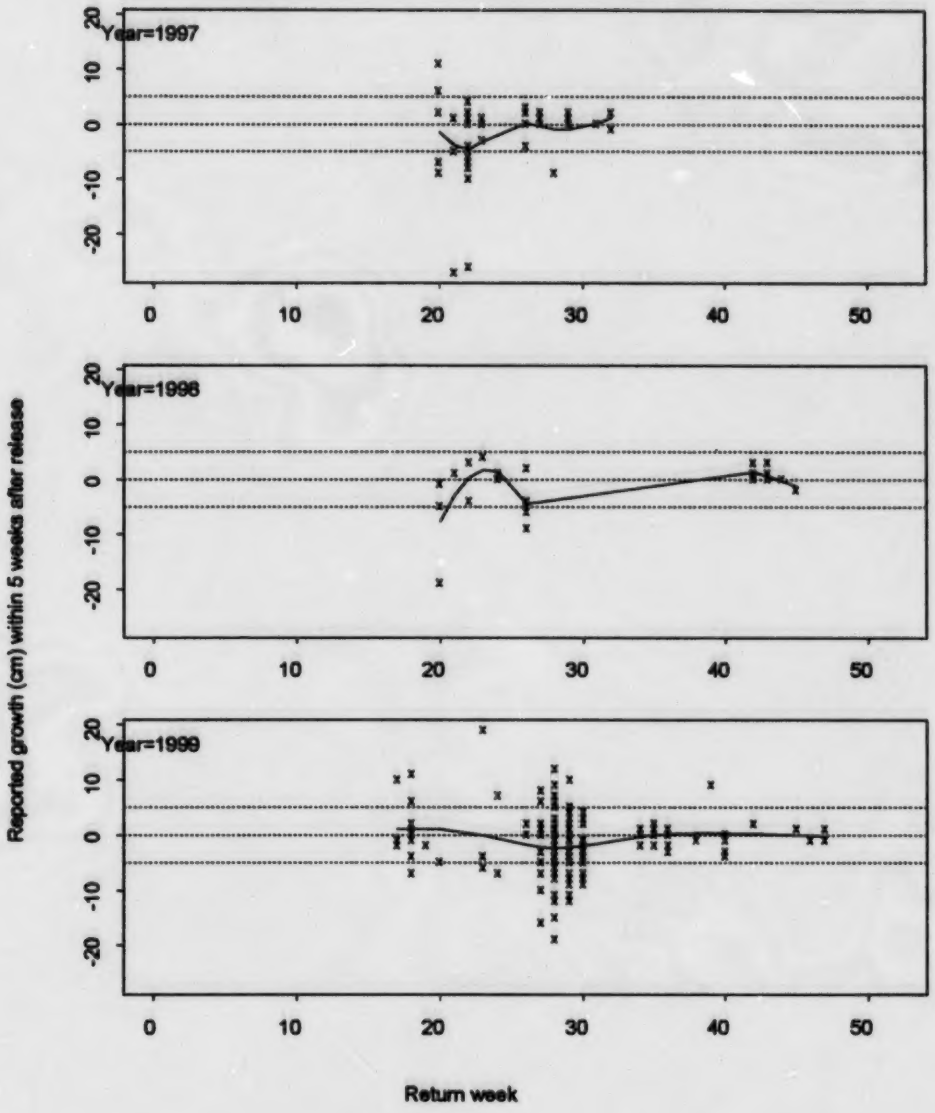

Figure 7: Bias in growth increments reported by the commercial fisheries in 3PS and 3KL during 1997-1999, versus tag-return week. Each panel represents a year. The solid line marks a local linear smooth of the data. The dotted lines mark the -5, 0, and 5 cm growth increments.

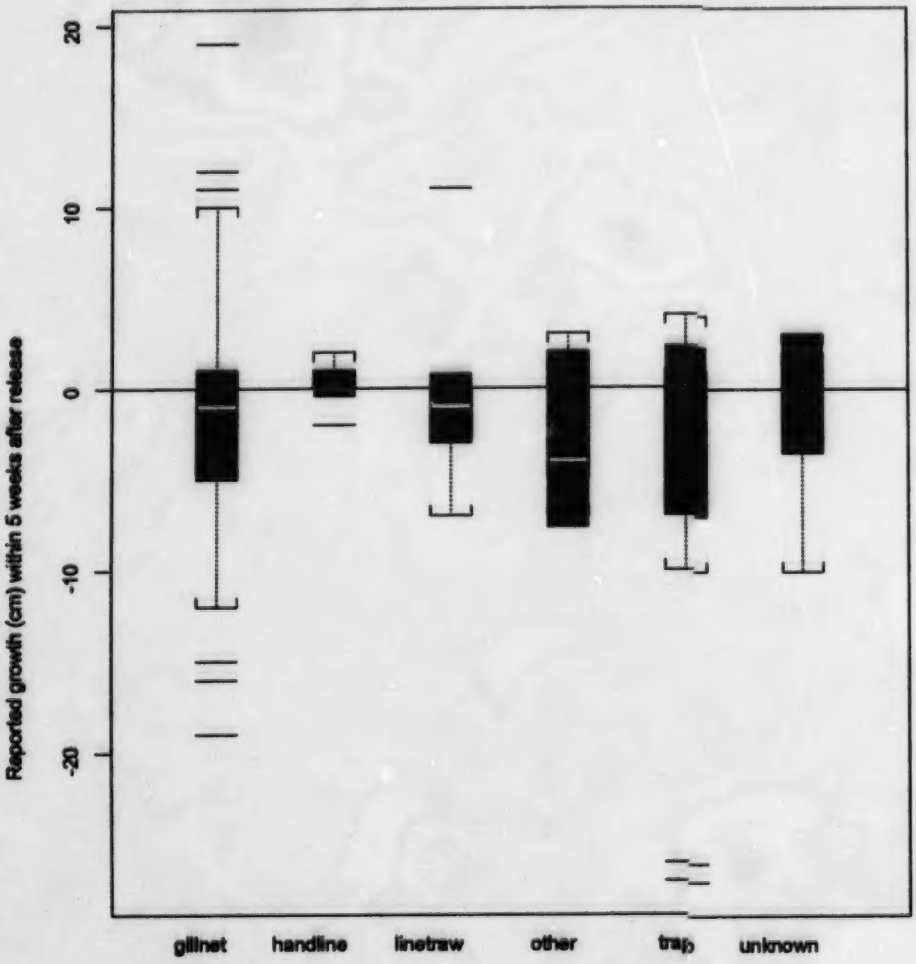

Figure 8: Bias in growth increments reported by the commercial fisheries in 3PS and 3KL during 1997-1999, as a function of gear type.

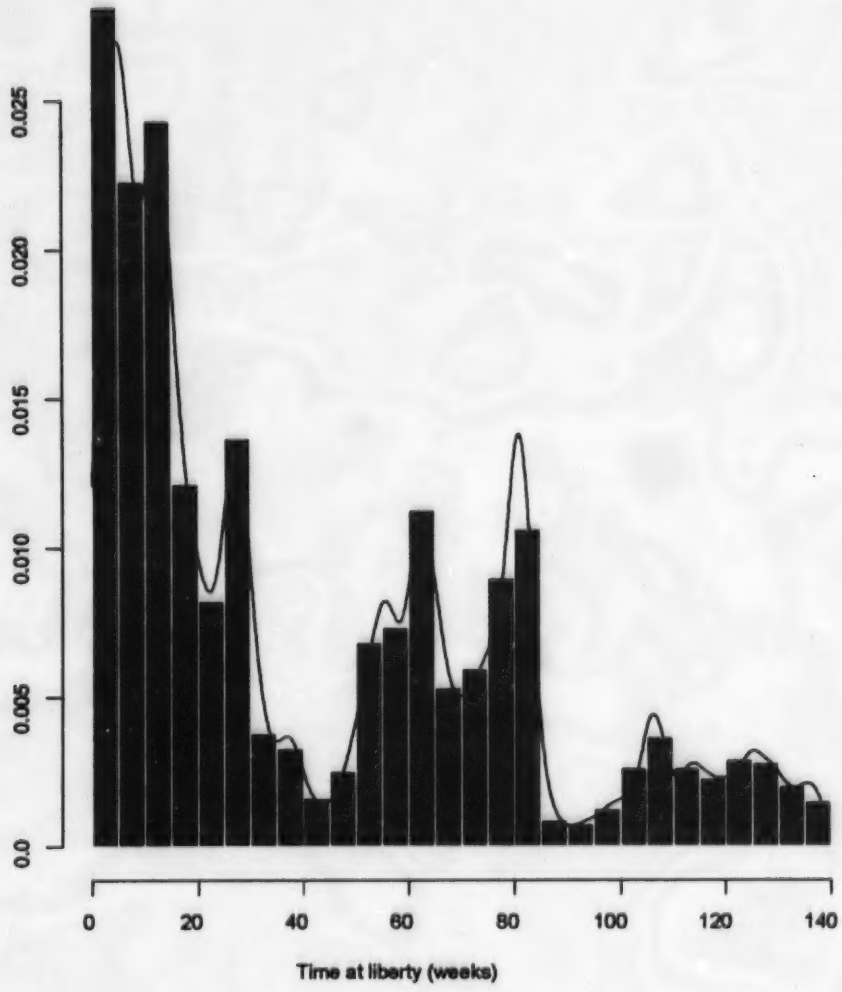

Figure 9: Frequency distribution of time-at-liberty. The solid line is a nonparametric kernel estimate of the density function, based on a bandwidth of 5 weeks.

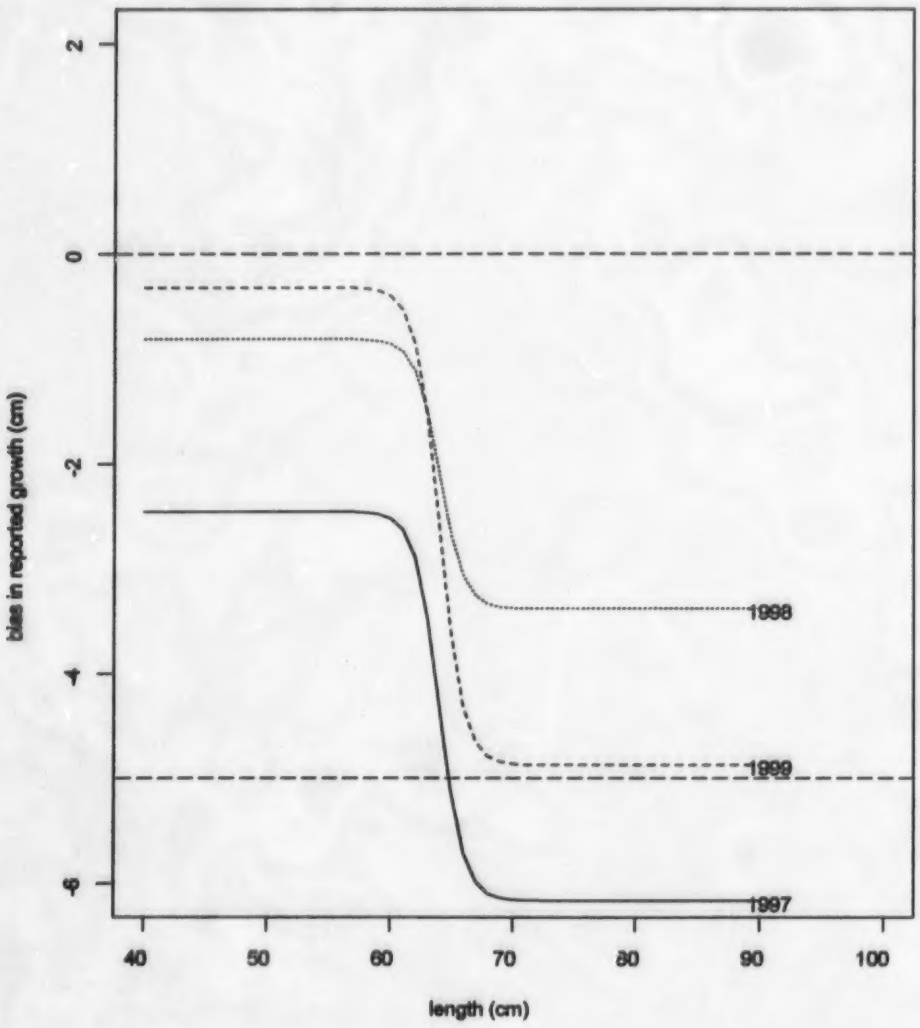

Figure 10: Estimates of the bias in growth increments reported by the commercial fisheries in 3PS and 3KL during 1997-1999, based on the annual Von Bertalanffy growth model. The dotted lines mark the -5 and 0 cm growth increments.

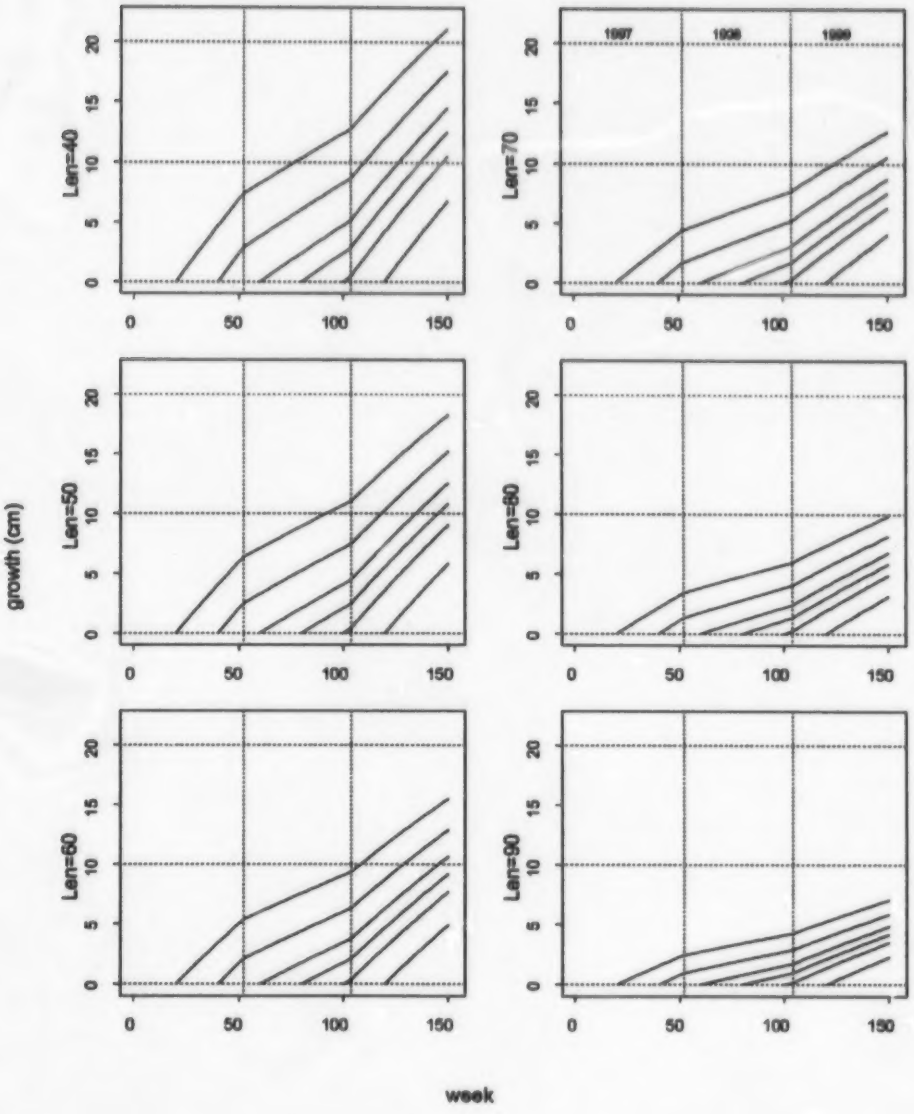

Figure 11: Estimated growth rates for cod in 3PS and 3KL during 1997-1999, based on the annual Von Bertalanffy growth model. The time scale is weeks since the beginning of 1997. Each solid line represents the growth for a fish. The intersection of a solid line zero growth line (dotted) is the release week. Growth is estimated up to week 150 (mid Nov, 1999). Dotted lines mark 10 and 20 cm growth. The vertical dotted lines mark the year boundaries.

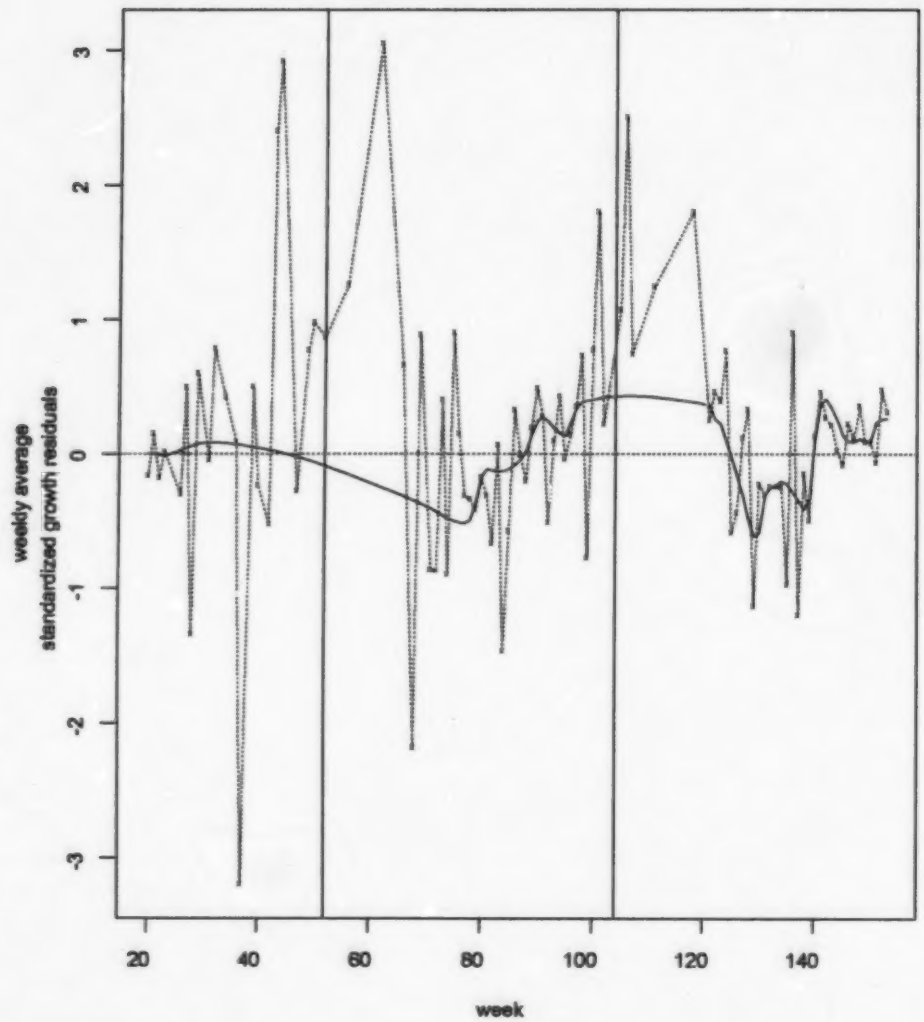

Figure 12: Weekly averaged standardized residuals (obs.-exp./std) from the annual Von Bertalanffy growth model. The dotted line joins the averages. The solid line represents a kernel smooth of the individual residuals. The vertical lines mark the bondaries between 1997-1998 and 1998-1999.

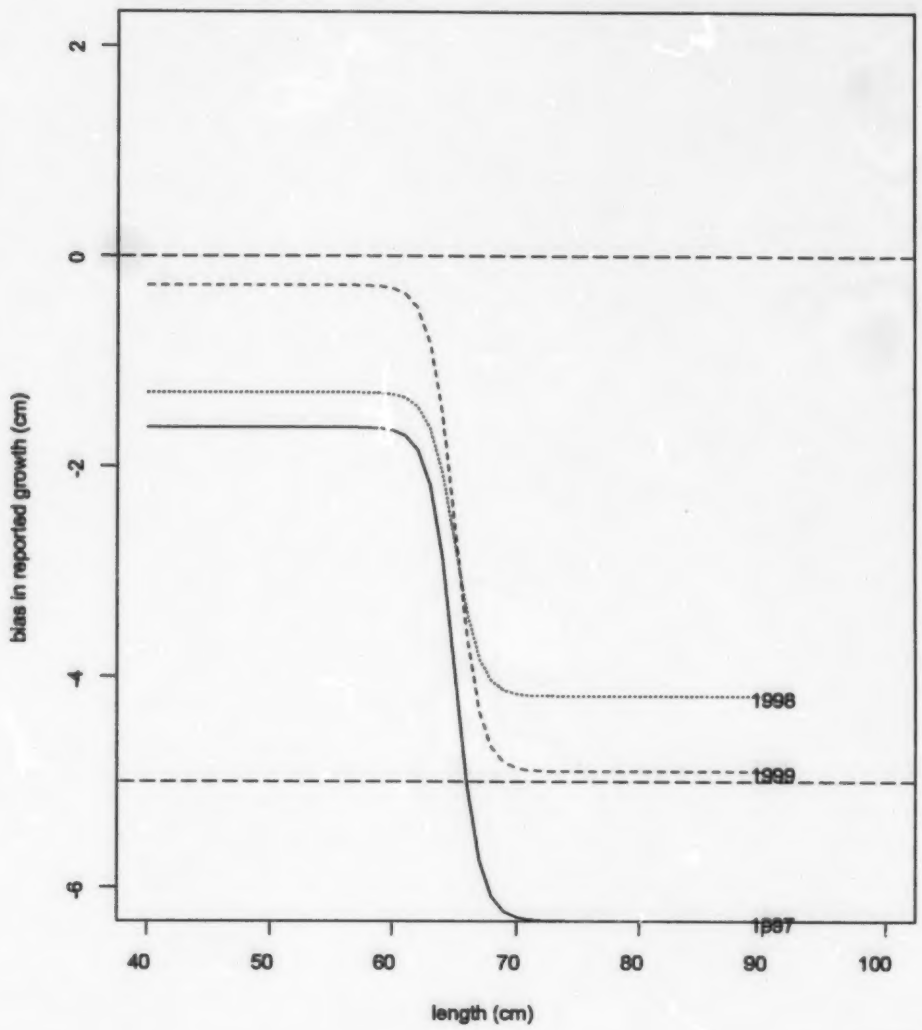

Figure 13: Estimates of the bias in growth increments reported by the commercial fisheries in 3PS and 3KL during 1997-1999, based on the seasonal Von Bertalanffy growth model. The dotted lines mark the -5 and 0 cm growth increments.

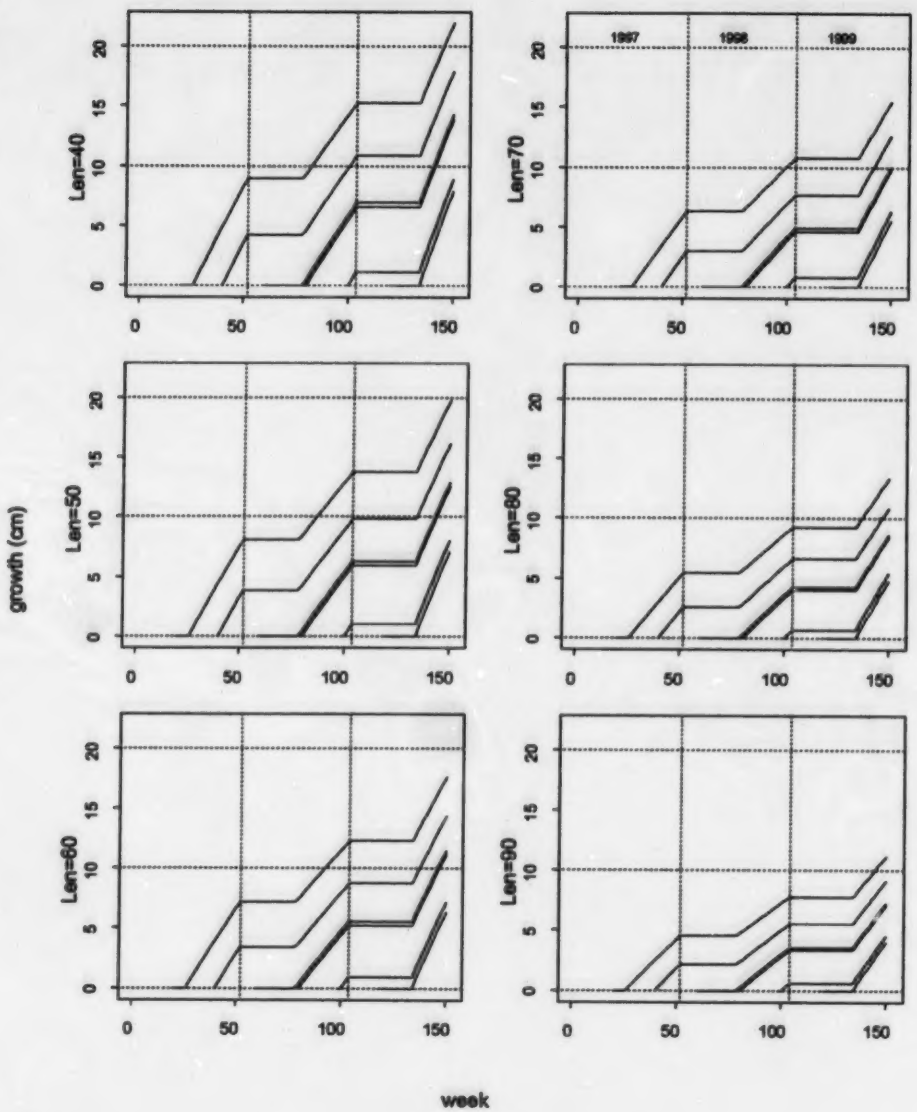

Figure 14: Estimated growth rates for cod in 3PS and 3KL during 1997-1999, based on the seasonal Von Bertalanffy growth model. The time scale is weeks since the beginning of 1997. Each solid line represents the growth for a fish. The intersection of a solid line zero growth line (dotted) is the release week. Growth is estimated up to week 150 (mid Nov, 1999). Dotted lines mark 10 and 20 cm growth. The vertical dotted lines mark the year boundaries.

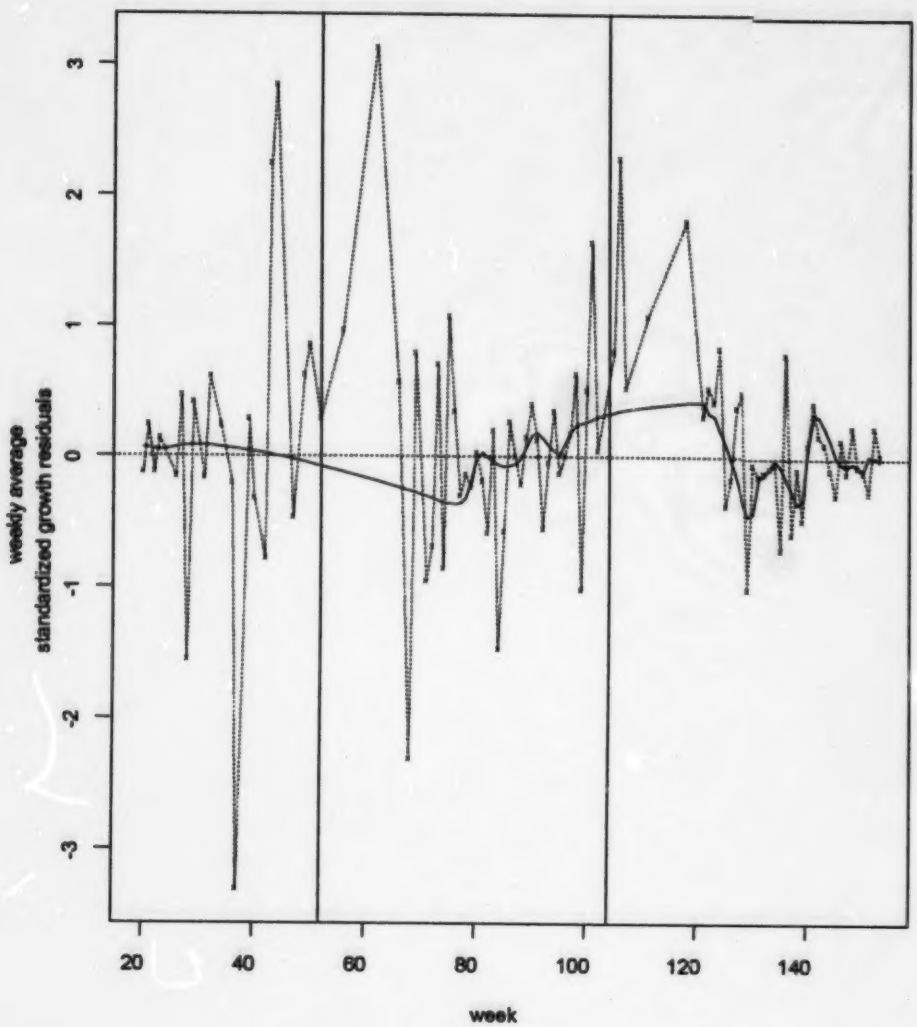

Figure 15: Weekly averaged standardized residuals (obs.-exp./std) from the seasonal Von Bertalanffy growth model. The dotted line joins the averages. The solid line represents a kernel smooth of the individual residuals. The vertical lines mark the bondaries between 1997-1998 and 1998-1999.

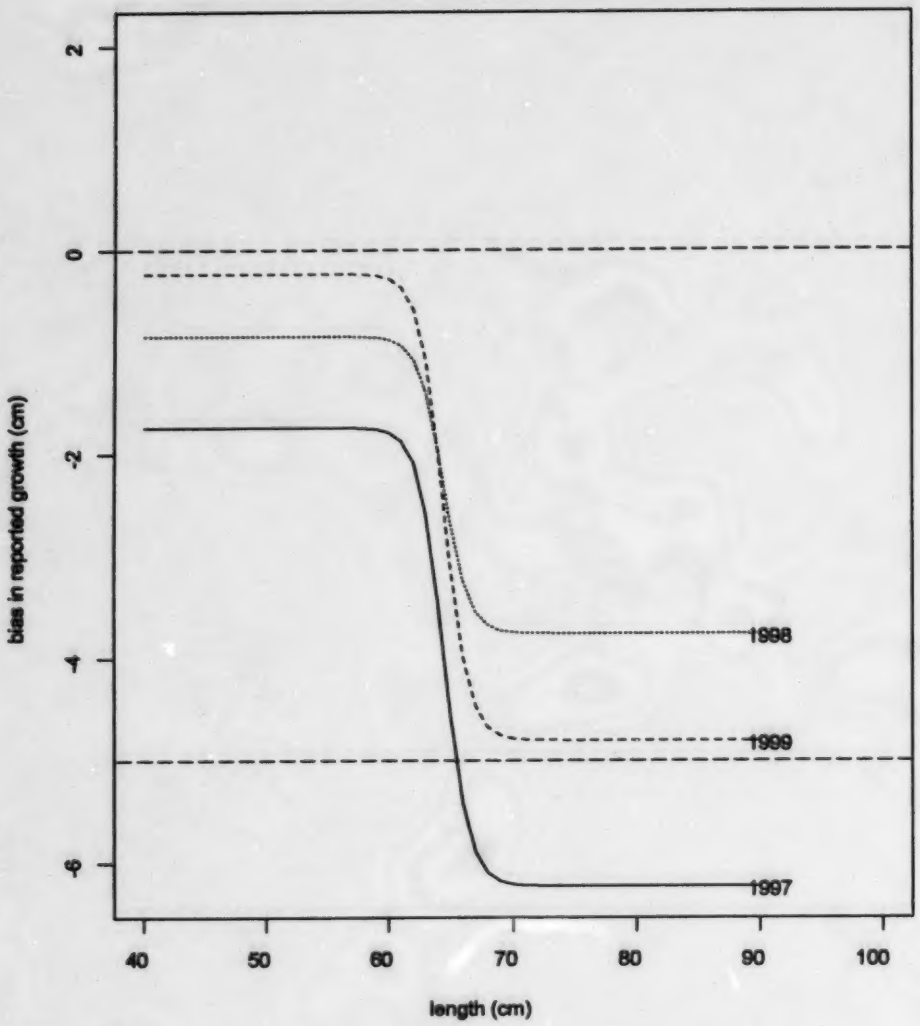

Figure 16: Estimates of the bias in growth increments reported by the commercial fisheries in 3PS and 3KL during 1997-1999, based on the seasonal Von Bertalanffy growth model with intrapopulation variability in λ_∞. The dotted lines mark the -5 and 0 cm growth increments.

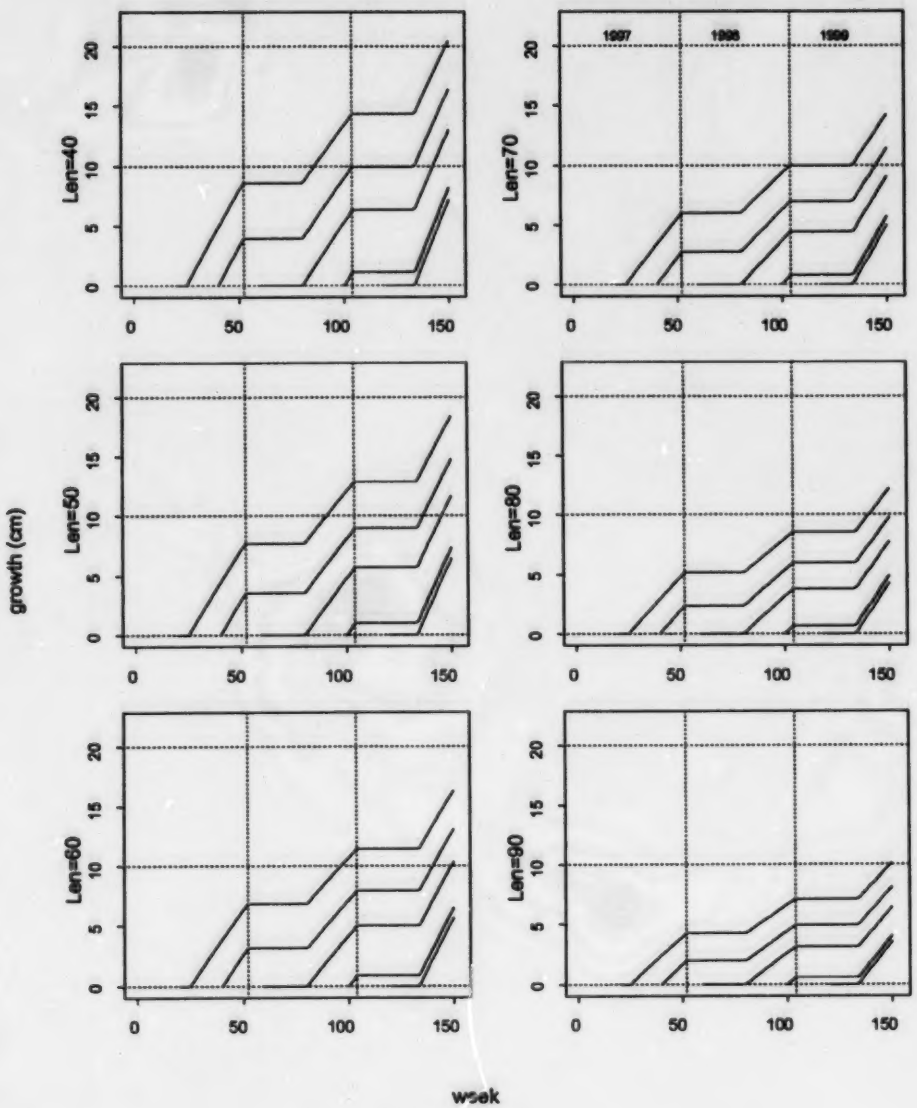

Figure 17: Estimated growth rates for cod in 3PS and 3KL during 1997-1999, based on the seasonal Von Bertalanffy growth model with intrapopulation variability in λ_{∞}. The time scale is weeks since the beginning of 1997. Each solid line represents the growth for a fish. The intersection of a solid line zero growth line (dotted) is the release week. Growth is estimated up to week 150 (mid Nov, 1999). Dotted lines mark 10 and 20 cm growth. The vertical dotted lines mark the year boundaries.

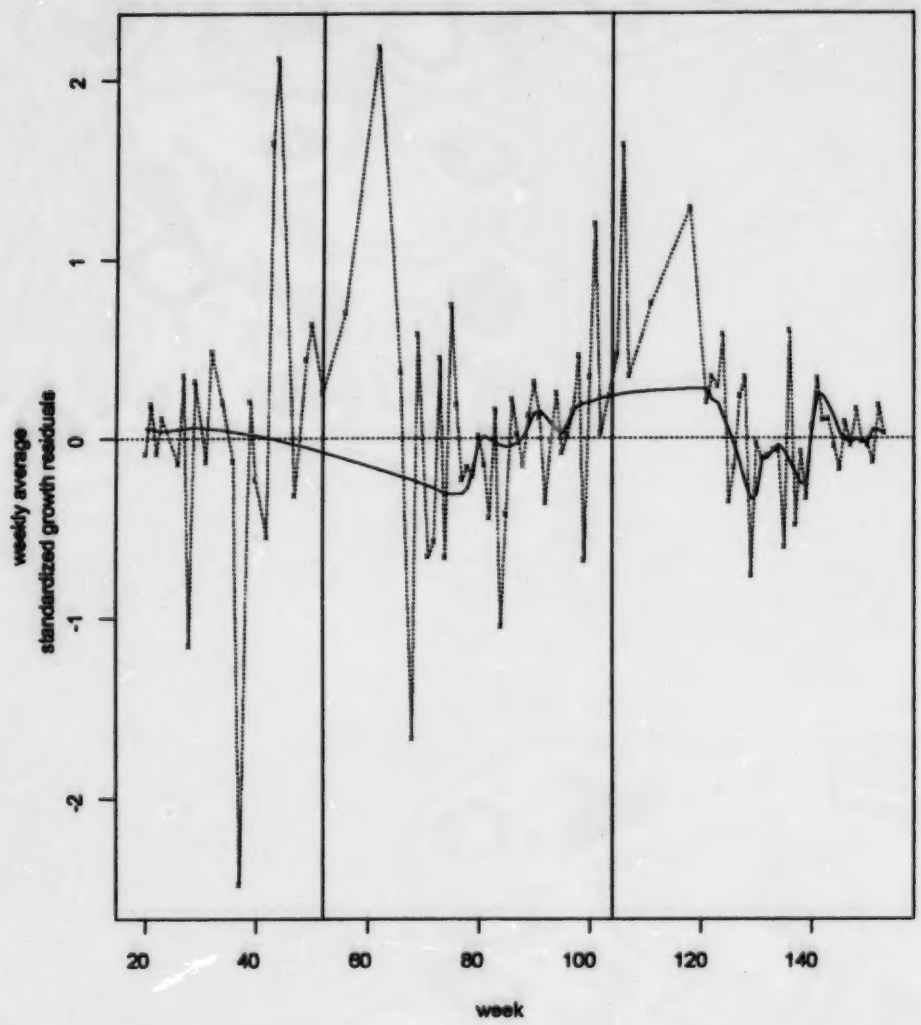

Figure 18: Weekly averaged standardized residuals (obs.-exp./std) from the seasonal Von Bertalanffy growth model with intrapopulation variability in λ_∞. The dotted line joins the averages. The solid line represents a kernel smooth of the individual residuals. The vertical lines mark the bondaries between 1997-1998 and 1998-1999.

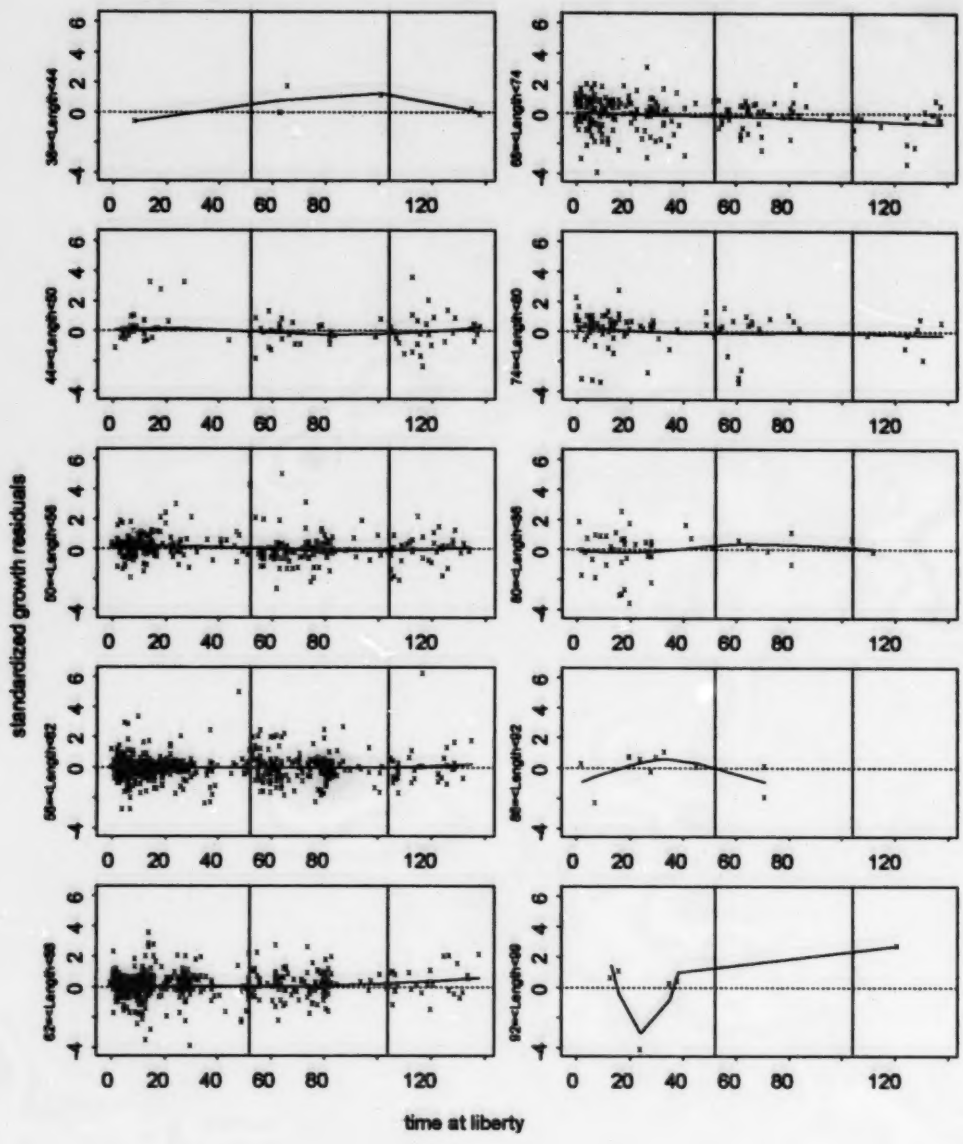

Figure 19: Standardized residuals (obs.-exp./std) from the seasonal Von Bertalanffy growth model with intrapopulation variability in λ_{∞}, versus time-at-liberty. Each panel is for a length class at release. The solid line represents a local linear regression smooth of the residuals. The dotted line is a horizontal line at zero. The vertical lines mark the boundaries between 1997-1998 and 1998-1999.

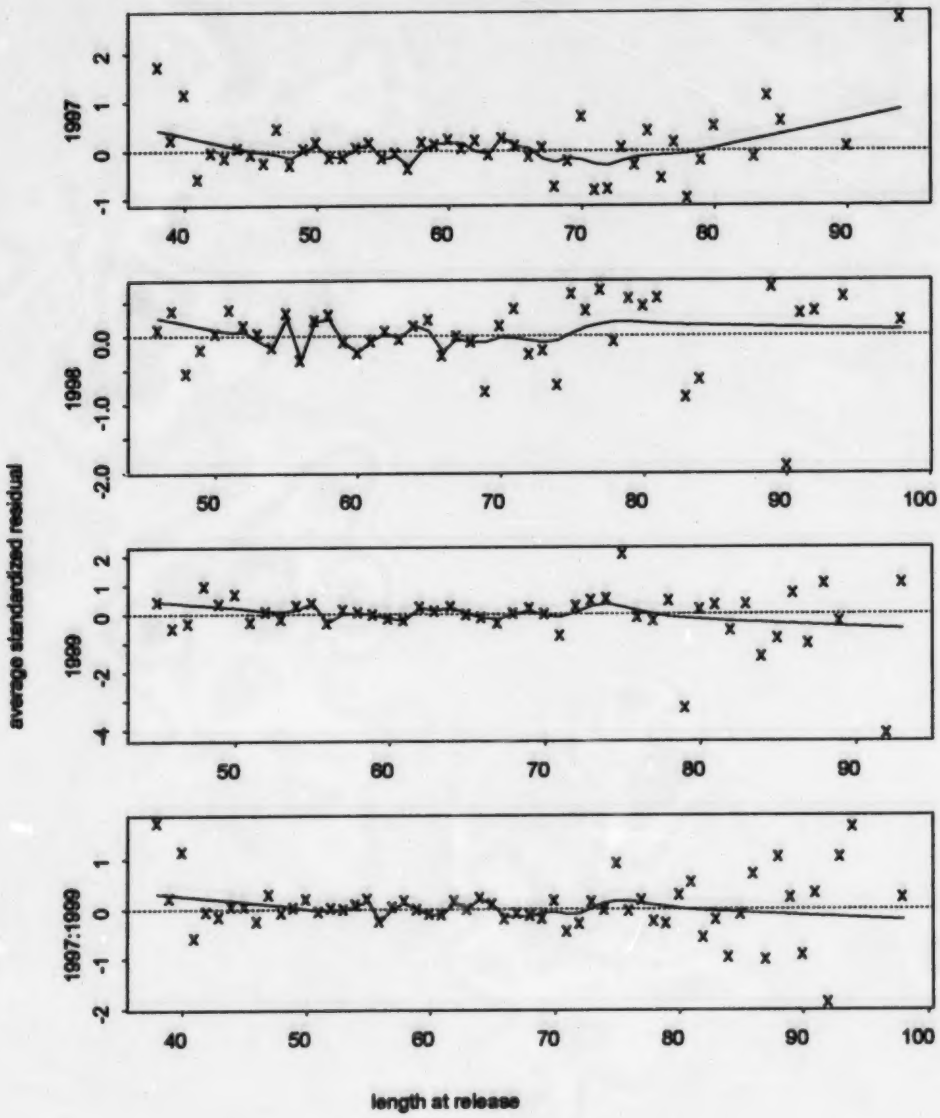

Figure 20: Average standardized residuals (obs.-exp./std) from the seasonal Von Bertalanffy growth model with intrapopulation variability in λ_{∞}, versus length-at-release. Residuals are averaged by one cm length classes. Each panel is for the release year, and the bottom panel is for all years. The solid line represents a kernel smooth of the residuals. The dotted line is the horizontal axis.

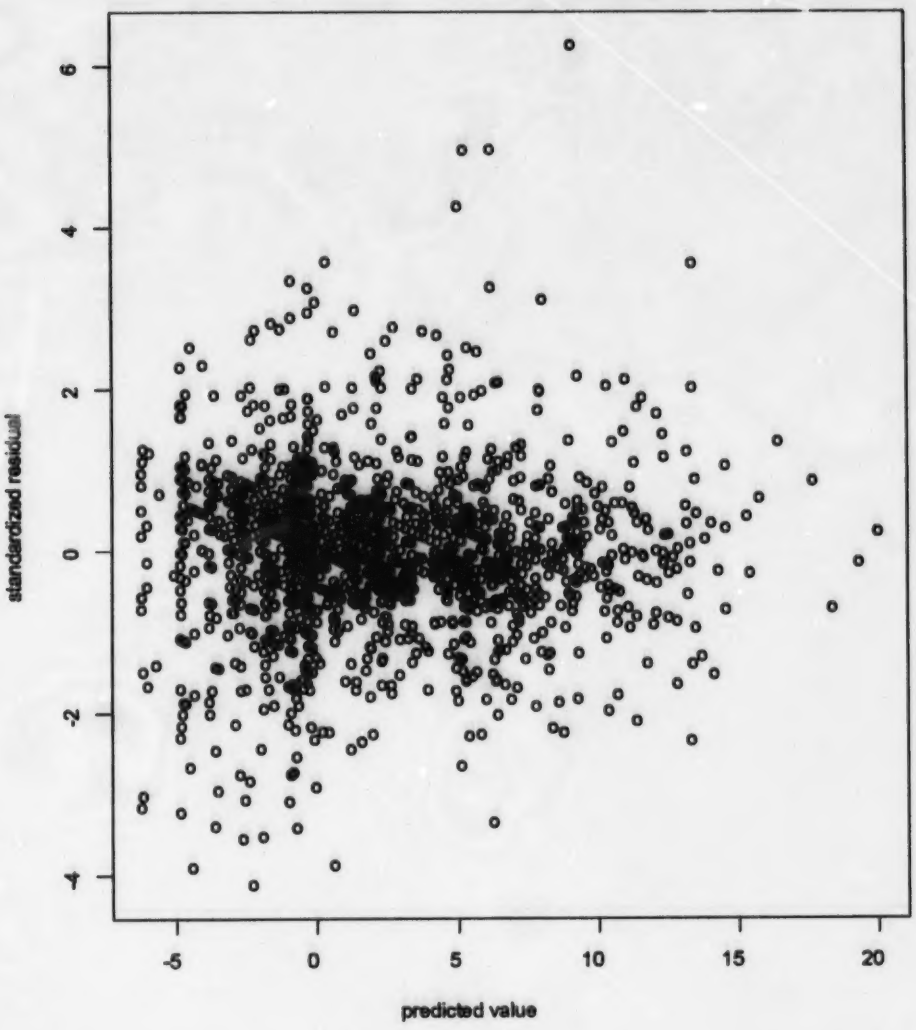

Figure 21: Standardized residuals versus predicted value, from the seasonal Von Bertalanffy growth model with intrapopulation variability in λ_∞